Vol. 9 JUNE · 1946 No. 2

# LLOYDIA

*A Quarterly Journal of Biological Science*

Published by the Lloyd Library and Museum, Cincinnati, Ohio

## The Adoxa Type of Embryo Sac: a Critical Review

P. MAHESHWARI

(*Dacca University, Dacca, India*)

CONTENTS



### I. INTRODUCTION

For many years the Adoxa type was considered the commonest of the tetrasporic embryo sacs, in which all four megaspore nuclei take part in the development. In this type there is only one division following megasporogenesis giving rise to an eight-nucleate embryo sac which organizes typically to form an egg apparatus of three cells and a group of three antipodal cells, leaving two free nuclei to function as polars. It was described almost simultaneously by Jönsson (1879/80) in *Adoxa moschatellina* and

Treub and Mellink (1880)in *Lilium* and *Tulipa*. Later, it was reported in a large number of other plants, belonging to various families of the Dicotyledons as well as Monocotyledons.

Bambacioni's (1928, a, b) researches disclosed, however, that the embryo sacs of *Lilium* and *Fritillaria* followed an entirely different mode of development. She found that immediately after the reduction divisions the megaspore nuclei take up a 1+3 arrangement, in which one nucleus lies at the micropylar end of the cell and three at the chalazal. In the next division, the three chalazal spindles fuse resulting in a second four-nucleate stage with two haploid nuclei at the micropylar end and two triploid ones at the chalazal. One more division follows, resulting in eight nuclei of which the four micropylar are haploid and the four chalazal are triploid.

This mode of development, characterized by the presence of four nuclear divisions between the megaspore mother cell stage and the mature embryo sac and the interpolation of a secondary four-nucleate stage, came to be known as the Fritillaria type. Subsequent work done by Bambacioni and several other embryologists in various parts of the world (see Maheshwari, 1946, for a full bibliography) showed that a number of plants, formerly supposed to have the Adoxa type of development, really belong to the Fritillaria type. Due to these corrections and transfers, the Fritillaria list gradually increased, while the Adoxa list continued to diminish, until it now contains only four genera.

## II. Known Distribution of the Adoxa Type

*Adoxa*.—Jönsson's original account of *Adoxa moschatellina* was confirmed in 1909 by Lagerberg and again in 1938 by Fagerlind. The four megaspore nuclei, produced as a result of the reduction divisions, show varying positions with respect to each other but eventually arrange themselves in two pairs at opposite ends of the embryo sac with a large vacuole occupying the space in the center. All of them divide once again. During this division the two polar spindles, one at each end, are oriented obliquely to the longitudinal axis of the embryo sac and are situated very close to the poles. The remaining two spindles, one at the chalazal and the other at the micropylar end, are in a direction more or less parallel to the longitudinal axis of the sac. As a result of this division there arise two very small nuclei at the micropylar pole and two similar ones at the chalazal, with two other pairs of larger nuclei, situated closer to the center. The two small ones at the micropylar end form the synergids, and of the larger, one becomes the upper polar and the other organizes into the egg cell; at the chalazal end the two small nuclei and one of the larger two give rise to the antipodals while the remaining nucleus functions as the lower polar. Sometimes the lowest chalazal nucleus of the four-nucleate stage is unable to complete its division so that there is a seven-nucleate embryo sac with only two antipodal cells.

*Sambucus*.—Lagerberg (1909) reported the same type of development in *S. racemosa*. This has now been confirmed by Fagerlind's (1939) study of *S. canadensis* and *S. ebulus*. A peculiarity in this case is the early vacuolation which is appreciable even at the megaspore mother cell stage, although in most other cases it commences only after megasporogenesis is completed.

*Erythronium*.—In 1901, Schaffner reported that in *Erythronium albidum* and *E. americanum* the four megaspore nuclei were not separated by walls and divided just once to produce an eight-nucleate embryo sac of the Lilium type[1] (=Adoxa type in present terminology.) On the basis of Hrubý's (1934, 1938) work on *E. dens canis*, which indicated the occurrence of the Drusa or Fritillaria type in this genus, Schaffner's account was considered somewhat doubtful (Maheshwari, 1937; Fagerlind, 1938, 1939). However, Cooper (1939) has recently confirmed the occurrence of the Adoxa type at least in *E. albidum*. He counted twenty-two pairs of chromosomes at the diakinesis stage as well as the heterotypic metaphase. The two nuclei formed as a result of the division had 22 chromosomes each. The spindles of the homotypic division were oriented obliquely to the longitudinal axis of the cell. After the formation of the four megaspore nuclei the cell was found to grow in size and elongate to a considerable extent becoming four times longer than broad and the cytoplasm in the middle region became highly vacuolate. The two micropylar nuclei and the upper chalazal nucleus divided normally and 22 chromosomes were agian counted on each equatorial plate. Only the nucleus nearest to the chalazal end was observed to undergo a more or less abortive division. Four nuclei were nevertheless formed at each pole of the embryo sac which organized in the usual fashion, viz., an egg apparatus of three cells, a group of three antipodal cells and two polar nuclei.

Referring to Schaffner's (1901) statement that "the egg apparatus is not very definitely organized,"[2] Cooper (1939, p. 865) says that in his material also a definite organization of the embryo sac was seen only for a short time and, if fertilization failed to take place, the membranes delimiting the cells broke down and all the eight nuclei became free. Such aborting embryo sacs were quite frequent. It is interesting to note that the polar nuclei and the nuclei of the egg and synergids were found to undergo a considerable increase in size before their final disintegration.

It is now probable that Schaffner (1901) was also correct in his account of *E. americanum*, but this needs confirmation.

*Tulipa*.—A very peculiar type of development has been described in *T. sylvestris* (Bambacioni-Mezzetti, 1931). Vacuolation frequently com-

[1] The designation "Lilium type," so common in older literature, has now been abandoned, as the embryo sac of *Lilium* has a different mode of development called the "Fritillaria type."

[2] Schaffner (1901, p. 380) considers this lack of organization of the egg apparatus as the usual thing in Liliaceae, but there seems to be no evidence in favor of such a supposition.

mences even at the megaspore mother cell stage and all four megaspore nuclei gather at the micropylar end of the cell, where they divide to give rise to a group of six cells (one of which is to be interpreted as the egg) and two free nuclei.

*T. tetraphylla* is essentially similar (Romanov, 1938) although in this case vacuolation commences after the four megaspore nuclei have been formed. Three of these gather in the micropylar part leaving only one in the chalazal (a reversal of the situation occurring in the Fritillaria type). All divide once again so that there are six daughter nuclei in the upper part of the sac and two in the lower. Cell-plates are laid down at the conclusion of the division, resulting in the formation of five cells at the microyplar end and one at the chalazal, leaving two free nuclei (the polars) in the center. Of the five micropylar cells one is the egg; the single antipodal cell soon degenerates.

In *T. ostrovskiana*, also investigated by Romanov (1938), some of the ovules show the same type of development as that described above for *T. tetraphylla* but usually the megaspore nuclei arrange themselves in two pairs, one at the micropylar end and the other at the chalazal. The next division gives rise to two quartets which organize into a three-celled egg apparatus, a group of three ephemeral antipodal cells and two polar nuclei.

The unipolar development seen in *T. sylvestris* and *T. tetraphylla*, belonging to the Eriostemones section of the genus *Tulipa*, is designated by Romanov as the Eriostemones Form of the Adoxa type.

### III. Irregular Occurrence of the Adoxa Type

The four genera, discussed above, i.e., *Adoxa*, *Sambucus*, *Erythronium* and *Tulipa*, are the only ones in which the Adoxa type is now known to occur with certainty but not even all species of the last two genera follow this mode of development. Thus, *Erythronium helneae*, *E. tuolumnense* and *E. japonicum*[3] definitely come under the Fritillaria type (see Maheshwari, 1946, for fuller information). *Tulipa maximoviczii*, *T. gesneriana*, *T. praecox* and *T. "Inglescomb Yellow"* belong to the Fritillaria type; and *T. rosea* to the Drusa type (Romanov, 1939a, b).

We shall now consider certain species in which the Adoxa type occurs sporadically in a small percentage of the ovules, although they usually follow some other type of development.

*Ulmus*.—This genus shows a considerable variability regarding the development of the embryo sac. Shattuck (1905) reported the Adoxa type in

[3] In another species, *E. dens canis*, investigated by Hrubý (1934, 1938), the position is not yet clear. In all probability, it follows the Fritillaria type, but Hrubý saw one stage showing two nuclei at the micropylar end and six at the chalazal. If another division took place in such an embryo sac, the development would be of the Drusa type, similar to that reported in *Majanthemum bifolium* by Stenar (1934).

*U. americana* but observed that "in very many cases" there seemed to be a further nuclear division. He frequently saw as many as 12 nuclei (occasionally more) evenly distributed and very similar in appearance. Later, a number of embryo sacs were found having four nuclei in the micropylar and eight or more in the chalazal end of the sac. Therefore, he concluded that the embryo sac of *Ulmus americana* was in some ways intermediate between "the regular eight-nucleate angiosperm type and the sixteen-nucleate sac of Peperomia." Leliveld (1935), who investigated *U. hollandica belgica*, *U. wilsoniana* and *U. pumila*, believed the development to be of the Adoxa type "with the restriction that the number of antipodal cells has augmented." Similarly, Miss Walker (1938) reported the Adoxa type in *U. fulva* but noted having seen 12 nuclei in one embryo sac.

Fagerlind (1938) saw a young embryo sac of an undetermined species of *Ulmus* with two nuclei at the micropylar end and six at the chalazal, and several mature ones with always more than three antipodals. He therefore interpreted the embryo sac to be fundamentally sixteen-nucleate although admitting the possibility of some reduction owing to a failure of some of the divisions at the chalazal end.

Ekdahl (1941) studied *Ulmus glabra* and figured a complete series of stages supporting Fagerlind's interpretations. The megaspore nuclei show a 1+3 arrangement, followed after the next division by a 2+6 stage. In the fourth and the last division the two lowest nuclei at the chalazal end remain quiescent so that the mature embryo sac has only 14 nuclei, four at the micropylar and ten at the chalazal. Very often the latter degenerate so that the mature embryo sac has only two to four antipodal cells. Those, which do remain however, enlarge and frequently assume an egg-like appearance, also observed by Shattuck (1905) and Leliveld (1935), sometimes even giving rise to embryos. In certain other cases the egg apparatus was seen to consist of more than three cells which may be due either to a secondary division of one of the original cells or to an abnormal distribution of the nuclei so that more than four came to lie at the micropylar end (Ekdahl, 1941, p. 153).

D'Amato's (1940) work on *U. campestris* revealed a somewhat different condition. He found that the megaspore nuclei may take up either a 1+3 or a 2+2 arrangement. The former condition was the more common (occurring in 65% of the ovules), and in this case the egg apparatus differentiated after four divisions of the megaspore mother cell (Drusa type) with some reduction in the number of nuclei at the chalazal end (10, 12 and 14 nuclei were counted in mature embryo sacs). When the latter condition occurred (35% of the ovules), there were only three divisions and the embryo sac was eight-nucleate (Adoxa type).

This is an interesting observation which helps us to understand the divergent reports of Stattuck, Leliveld and Walker on the one hand, and of

Fagerlind and Ekdahl on the other. It now seems that in this genus the Drusa form of development is the rule but that the Adoxa type also occurs quite frequently. Accordingly, the earlier authors were at least partially correct, although further work is of course necessary to clear this point.

*Tamarix.*—Mauritzon (1936a) reported the Adoxa type in six species of this genus, namely *T. tetrandra*, *T. aestivalis*, *T. africana*, *T. gallica*, *T. odessana* and *T. pentadra*. Later workers (Joshi and Kajale, 1936; Sharma, 1936) demonstrated that in the species studied by them development follows the Fritillaria type. Subsequent investigations by Puri (1939) on *T. chinensis*, Pároli (1940) on *T. gallica* and Battaglia (1941) on *T. africana* have shown however that while development is usually of the Fritillaria type, deviations are possible and the Adoxa type also occurs in a certain percentage of the ovules. Mauritzon does not seem to have been aware of Bambacioni's (1928a) work on *Fritillaria* at the time of writing his paper and his statement, that in the species studied by him the antipodals were sometimes ephemeral but on other occasions quite large and persistent, may perhaps find an explanation in the two different modes of development occurring in this genus. If the development is of the Fritillaria type, the antipodal cells will be triploid and are then likely to be better developed and more resistant to decay than in those cases in which it follows the Adoxa type and the chromosome number remains unchanged. However, this is only a possible interpretation and a reinvestigation is necessary to confirm it.

*Armeria.*—All species of this genus, which have so far been investigated, have a Fritillaria type of embryo sac. In *A. vulgaris*, D'Amato (1940a) has found that in approximately 3% of the ovules the development may proceed according to the Adoxa type.

*Leontodon.*—Bergman (1935) found some very interesting embryological variations in *Leontodon hispidus*. One individual designated as 1931:123 was found to be partially apomictic. The second (1931:123x) was found to have a multicellular archesporium and a large complex of embryo sacs of monosporic origin which penetrated deep into the chalaza and had a variable number of nuclei lacking any regular arrangement or organization. The third (1931:284) showed weakly developed somatic apospory. In this case, microspore formation was usually seen to proceed normally, but in more than half the ovules the walls separating the four megaspores became mucilaginous and dissolved away so that the nuclei came to lie in a common cavity. Only one more division took place giving rise to the eight nuclei of the mature embryo sac. Under such conditions the development would be of the Adoxa type.

However, several deviations from this method were also observed. Thus, some embryo sacs were found to have as many as 14 nuclei. Bergman believes that in such cases there was a fourth division but the dissolution of

the wall between the third and the fourth megaspore and consequently the incorporation of the lowest megaspore nucleus were delayed until the upper three megaspore nuclei had already undergone one division. This gave a seven-nucleate stage which by further division formed a 14-nucleate embryo sac.

In certain other cases diploid embryo sacs were found to originate by a dissolution of the wall separating the dyad cells and the formation of a restitution nucleus. A full discussion of these events is outside the scope of this paper.

*Rudbeckia.*—Most of the species, belonging to this genus, show the Fritillaria type of embryo sac but Rosén (1944) has recently reported the occurrence of the Adoxa type in one form of *R. laciniata*, collected in the Botanical Garden at Gothenburg. Another form of the same species showed the Fritillaria type. Fagerlind (1944, p. 30), on the other hand, reports the possibility of the formation of restitution nuclei. Further work is necessary to clear up the development of the embryo sac in *R. laciniata*.

## IV. Excluded and Doubtful Cases

We now proceed to consider those cases which were formerly believed to have an Adoxa type of embryo sac but which must now be deleted from that list either because of recent reinvestigations or because of other indirect and circumstantial evidence. Of special interest in this connection is the paper by Fagerlind (1939), comprising a critical review of the older literature on this subject and a fresh study of some doubtful species. In the following pages frequent reference will be made to this contribution as well as some others (Fagerlind, 1938, 1944; Maheshwari, 1937, 1941). Before discussing individual cases of this type, it is necessary however to call attention to some general characteristics of the Adoxa type of development which serve to distinguish it from the other types with which it has been most frequently confused. This will enable the reader to appreciate some of the points which are bound to come up quite frequently during the present discussion.

Since the Fritillaria type has often been mistaken for the Adoxa type owing to the fact that in both cases the final stage is eight-nucleate, it may be pointed out that the former is characterized by two four-nucleate stages. In the first or *primary* stage all nuclei are of approximately the same size and in the next or *secondary* stage the two chalazal nuclei are triploid and therefore of a much larger size.[4,5] In the Adoxa type, on the

[4] In certain exceptional cases, the three chalazal nuclei of the primary four-nucleate stage are reduced in size from the very beginning and therefore the secondary four-nucleate stage does not show the usual size difference between the micropylar and chalazal nuclei (for literature and details, see Maheshwari, 1946).

[5] Occasionally, there is also a secondary two-nucleate stage. In such cases the fusion of the

other hand, only one four-nucleate stage is present and typically all nuclei are approximately of the same size and shape.

In other cases, the four nucleate stage of a monosporic embryo sac has been mistaken for the same stage of a tetrasporic one. This is possible when the dyad and tetrad stages of the monosporic type are entirely overlooked due to inadequate material or hasty observation. In some cases the remains of the three degenerating megaspores, characteristic of a monosporic embryo sac, become absorbed and obliterated at a very early stage and increase the chances of error. Nevertheless, a careful observer has another test at his disposal. During the meiotic divisions and up to the formation of the megaspores (or megaspore nuclei) the cytoplasm of the cells concerned (i.e., the megaspore mother cell or its derivatives) exhibits a more or less homogeneous structure with only small and inconspicuous vacuoles. It is only after the completion of megasporogenesis that a conspicuous vacuolation is discernible. For this reason, the two- and four-nucleate stages of a monosporic embryo sac always show a large central vacuole, while this is hardly ever the case in tetrasporic embryo sacs where vacuolation typically commences only when the four-nucleate stage is passing into the eight-nucleate (Fig. 1).

We shall now deal with those cases whose embryo sac development was incorrectly interpreted as following the Adoxa type, or is open to question on very valid grounds.[6]

## PIPERACEAE

In two genera of this family, *Piper* and *Heckeria*, Johnson (1902, 1910) reported the development of the embryo sac to be of the Adoxa type. The writer (Maheshwari, 1937) reinterpreted his illustrations in the light of the newly discovered Fritillaria type and further investigations made since then on several species have fully justified the opinions expressed at that time (see Maheshwari, 1946, for additional references). The only exception is an undetermined species of *Piper* (*Piper* sp. Bogor Nr. IV C 45) recently studied by Fagerlind (1939) which behaves differently in that two of the megaspore nuclei degenerate, and the remaining two alone divide to give rise to an eight-nucleate embryo sac. Nuclear fusions of the Bambacioni type are absent and, strictly speaking, the embryo sac is bisporic. Palm's (1915) fig. 10a of *Piper subpeltatum* is also interpreted by Fagerlind in the same way; (the two prominent nuclei, separated by a large vacuole, are

---

three chalazal megaspore nuclei occurs before they have progressed beyond the prophase stage of the next division.

[6] In the following treatment, the families have been arranged according to the system given by Engler (1936). This is done purely for the sake of convenience, and the writer does not necessarily endorse all their views regarding the inter-relationships of individual orders and families?

considered to be the surviving megaspore nuclei left over after the other two have degenerated and disappeared).

It would be of interest to investigate other species of these two genera, keeping in mind the possibilities of such variations. Meanwhile, no species of either *Piper* or *Heckeria* is now known to have the Adoxa type of embryo sac.

## SALICACEAE

Chamberlain (1897) studied five species of *Salix*, particularly *S. petiolaris* and *S. glaucophylla*. He reported (p. 6) that "almost always" the

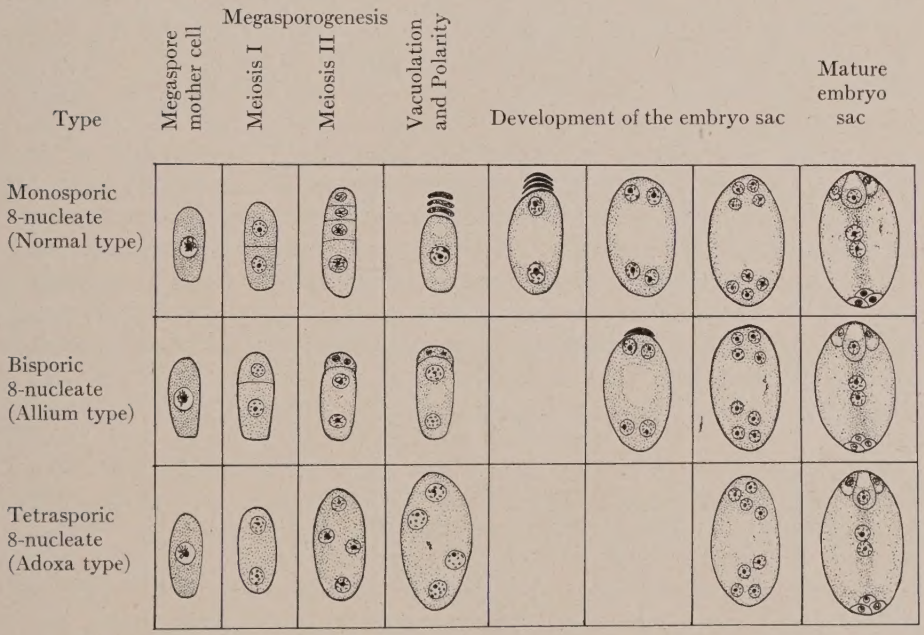



FIG. 1. Diagram to show stage at which vacuolation begins in the development of monosporic, bisporic, and tetrasporic embryo sacs. Note the difference between the two- and four-nucleate stages of the monosporic and terasporic embryo sacs.

megaspore mother cell "divides into two cells, a smaller one nearer the micropyle, and the larger one which becomes the fertile macrospore. The smaller cell either undergoes one transverse division, thus giving rise to two potential macrospores, or it does not divide at all. In a case like fig. 17 there is a possibility that the two smaller cells may have been cut off in succession from the larger cell, but as no mitotic figures were found in this stage this question cannot be settled." Elsewhere he says: "Sometimes the macrospore mother cell does not divide but develops directly into the

macrospore. If any potential macrospores have been cut off, they are crowded and absorbed by the growing fertile macrospore until nothing remains of them but a refractive cap, and even this soon disappears."

The picture that one gets from these vague statements is that the embryo sac may develop in any one of three possible ways: Normal type, Allium type and Adoxa type. Earlier, Jönsson (1879/80) reported Normal type in *S. fragilis* and *S. aurita*, and Håkansson (1929) confirmed this in *S. viminalis* and *S. caprea*. Fagerlind (1938, p. 465), who has discussed this question in detail, believes that the development follows the Normal type and that the occurrence of the Allium and Adoxa types has not been established in any species of *Salix*. I am in agreement with him and wish to point out that Chamberlain's fig. 17, interpreted by him as a functioning dyad cell with two degenerating cells on top (products of division of the upper dyad cell, according to him) probably shows instead the degenerating upper dyad cell and the two megaspores derived from the lower dyad cell of which the chalazal one is enlarging. Or perhaps, the tetrad was T-shaped and one of the megaspores was lying in an adjoining section so that only a row of three cells was visible. From Chamberlain's statements it appears that he did not consider it to be of much importance to establish whether the embryo sac developed by one method or the other. Incidentally, another point which deserves further study, is his statement (p. 172) that "in a few cases the synergids were observed to persist until the embryo was almost in the cotyledon stage."

### JUGLANDACEAE

Karsten (1902) studied a number of plants belonging to this family, viz., *Juglans nigra*, *Pterocarya fraxinifolia*, *Carya amara* and *C. tomentosa*, but was apparently unable to decide whether the development follows the Normal or Adoxa type. At one place he writes (p. 318): "diese (i.e., the megaspore mother cell) wird ohne weitere Zelltheilungen und Verdrängungen direct zum Embryosack," but soon adds: "In anderen Fällen war aber auch eine eingetretene Theilung der Embryosackmutterzelle nachzuweisen, so dass drei oder vier Tochterzellen entstanden. Die beiden oberen habe ich niemals sich weiterentwickeln sehen, die beiden unteren schienen ziemlich gleiche Chancen zu besitzen." He also states that in *J. nigra* there is no fusion of the polar nuclei, or that if it does occur it is only at a very late stage.

Since then it has been shown, however, that the embryo sac is of the Normal type; see Nawaschin and Finn (1913) on *J. regia* and *J. nigra;* Langdon (1934) on *J. mandschurica* and *Carya glabra;* Nast[7] (1935) on *J. regia;* and Woodroof (1928) and Shuhart (1932) on *Hicoria pecan.*

[7] In Figs. 16 and 17 of Nast (1935), the cell considered to be a "macrospore" is more likely the megaspore mother cell in the meiotic prophase.

## Fagaceae

Conard (1900) investigated *Quercus velutina* Lam. (=*Q. coccinea tinctoria* Gray). His account is quite confused when he comes to the stages leading to megaspore formation and he regards all archesporial cells as "potential megaspores." Presumably he made no distinction between 'megaspore mother cell' and 'megaspore.' Fagerlind (1938, p. 465; 1939, p. 4) therefore remarks that "die Entwicklung des Embryosackes ist hier ganz unbekannt." In my opinion, however, Conrad's fig. 29 gives sufficient indication, that the development is of the Normal type. It shows two cells in the metaphase stage which could hardly be anything but the two dyad cells in the second reduction division. A two-nucleate stage is not figured but the prominent vacuolation seen at the four-nucleate stage (see figs. 30 and 31) strengthens the view that the embryo sac is monosporic and not tetrasporic.

## Santalaceae

*Thesium.*—The exact mode of development of the embryo sac of *Thesium* remained unknown for a long time. Jönsson's (1879/80) work on *T. intermedium* (now *T. linophyllon*) does not give anything clear or definite about the process of megasporogenesis. Guignard (1885) reported Normal type in *T. divaricatum*. Modilewski (1928), who investigated *T. intermedium*, apparently considered the development to be of the Adoxa type. Schulle (1933) said the same for *T. montanum* (now *T. Bavarum* Schrank): "Die Makrosporenmutterzelle wird ohne Teilung direkt zum Embryosack. Seine Bildung erfolgt nach dem *Lilium*-Typus."

None of the above investigators considered this point in detail, however. Rutishauser (1937) showed a normal tetrad of megaspores in *T. rostratum* with the chalazal megaspore functioning. Fagerlind (1939) found the same in *T. montanum* (=*T. Bavarum* Schrank). Further development is also normal except that there may be some reduction in the number of nuclei at the chalazal end owing to the inability of one of the nuclei in this region to divide after the four-nucleate stage; a noteworthy feature is the formation of an embryo sac caecum or haustorium which pushes onward leaving the antipodals in a lateral position.

More recently, L. N. Rao (1942) has investigated four Indian species of the Santalaceae: *Santalum album*, *Thesium wightianum*, *Osyris arborea* and *Scleropyrum wallichianum*. In every case a normal megaspore tetrad is formed with the only difference that in *Santalum* and *Scleropyrum* it is the micropylar megaspore which functions and not the chalazal. No member of the family Santalaceae is therefore now known to have an Adoxa type of embryo sac.[8,9]

[8] See also, in this connection, Schaeppi's (1942) work on *Thesium*.

[9] See p. 84.

## LORANTHACEAE

Billings (1933) investigated two species of *Phoradendron: P. villosum* and *P. flavescens* var. *macrophyllum*. There are two archesporial cells which function directly as the megaspore mother cells and the first division is heterotypic. No mention is made of the two- and four-nucleate stages but (p. 267) "after completion of the four-nucleate stage within the placenta, each embryo-sac develops what appears to be a haustorial growth, tubular in form, that passes laterally outwards, or else downwards, the direction depending on the depth of the space between the placental base and the carpels. After passing under this space, the growth turns sharply upwards within the tissue of the carpel." Two of the four nuclei accompany the outgrowth, keeping just back of its tip. Of these the upper is said to give rise to four daughter nuclei, which organize the egg and *three* synergids. The second nucleus divides to form two polar nuclei. These with the two nuclei which remain behind in the placental portion of the embryo sac form the eight nuclei of the mature embryo sac. Occasionally, however, the two placental nuclei also divide, in which case the embryo sacs are ten-nucleate.

The author (p. 266) concludes that *Phoradendron* belongs to the Lilium (=Adoxa) type of embryo sac development "in the main," "though the origin of the primary endosperm nucleus is different."

Maheshwari (1937) listed *Phoradendron* as one of the doubtful cases. Fagerlind (1939) is in agreement with this view but concedes nevertheless that the embryo sac is of a tetrasporic type: "In Billings Arbeit fehlen jedoch sichere Beweise dafür, dass der Embryosack wirklich tetrasporisch ist. Ich halte dies aber für so gut wie sicher, da nur in diesem Fall die Anzahl Teilungsschritte mit den bei früher bekannten Fällen (*Tanacetum*, *Crucianella*, *Ulmus* and *Limnanthes* have been mentioned) vorkommenden übereinstimmt und da der vierkernige Embryosack gar kein Vakuolisierung aufweist."

I am inclined to think, on the other hand, that the development is *not* of the tetrasporic type and Billings' account is questionable for the following reasons:

a. The embryo sac development in the other Viscoideae, so far investigated (for literature see Maheshwari, 1937, 1941), is of the Allium type with the upper dyad cell functioning.

b. Billings does not figure or describe the stages intervening between the

---

[9] It might be noted here that Rao (1942) supports the old view that the ovules of the Santalaceae are naked, that "definite seed coverings are not produced," and that the micropyle is a narrow passage through the nucellus. Judging from Schulle's and Fagerlind's figures, however, this view seems to be untenable. An integument *is* present although the nucellus is extremely reduced and soon becomes unrecognizable.

megaspore mother cell and the four-nucleate embryo sac and it seems quite possible that he missed some of them altogether.

c. His account of the origin of the last stage (eight- or ten-nucleate embryo sacs) is also doubtful, particularly in regard to the occurrence of three synergids and the peculiar mode of origin of the secondary nucleus.

Regarding Fagerlind's interpretation of the number of megaspore nuclei taking part in the formation of the embryo sac, it may be said that the lack of vacuolation seen in Billings' fig. 8 of the four-nucleate stage of *P. villosum* cannot be considered as an indubitable proof of its tetrasporic nature, for it is difficult to apply the usual criteria to a family like the Loranthaceae in which the embryo sacs often have an extremely abnormal and weird organization. In *Korthalsella dacrydii* also (Rutishauser, 1935), which has an Allium type of embryo sac, there is no appreciable vacuolation at the newly formed four-nucleate stage (see his figs. 7c, 8a, and 8b, embryo sac on left). Besides, the only four-nucleate stage figured by Billings for *P. flavescens* (see his fig. 10) does show very prominent vacuolation.

## Balanophoraceae

*Helosis.*—Umiker (1920) thought that *H. guyanensis* (now *H. cayennensis*) is an apomict and described the development as of the Adoxa type (without the occurrence of any reduction in the chromosome number). Fagerlind (1938a) has shown that he was mistaken in both respects, that reduction and fertilization occur normally and the development is of the Allium type. After the eight nuclei have been formed, the micropylar quartet gives rise to an egg apparatus and the upper polar nucleus. From the chalazal quartet, as a rule, two nuclei move up and fuse with the upper polar nucleus, and the remaining two form a single binucleate antipodal cell or two uninucleate ones. Sometimes, when there are only two polar nuclei, all three antipodals are formed.

*Balanophora.*—This genus has received the attention of several authors: Hofmeister (1858), Lotsy (1899), Treub (1898), Van Tieghem (1896, 1907), Ernst (1914), Kuwada (1928), Ekambaram & Panje (1935), Zweifel (1939), and Fagerlind (1945).

Of the older contributions, that of Ernst on *B. globosa* and *B. elongata* is the most important. He considered the development to be of the Adoxa type but figured some stages to show that under exceptional conditions the megaspore mother cell divides into two dyad cells of which one gives rise to the embryo sac, i.e., the development is then of the Allium type. After the two-nucleate stage the embryo sac undergoes a bend and assumes a horseshoe-shaped form with one pair of nuclei at each end. The next division gives rise to two quartets of which the one formed at the lower end (which, however, is now situated at a higher level) gives rise to the egg apparatus and upper polar nucleus.

In *B. dioica*, Ekambaram & Panje (1935) found that the first division of the megaspore mother cell results in the formation of a small lower dyad cell and a larger upper one. In the second division the two spindles are more or less at right angles to each other, that of the upper cell lying in the long axis of the cell. The result is a tetrad of megaspores of which the uppermost cell is the largest and gives rise to the embryo sac while the basal three soon begin to degenerate, although their remains are distinguishable for some time afterwards. According to these authors, therefore, the development is of the monosporic type. Their account is nevertheless confused by a later statement (p. 540): "It must, however, be pointed out with equal emphasis that one now and then comes across a more or less fully developed embryo-sac with no evidence of degenerating megaspores at its base. . . . These instances, by no means to be overlooked, make it impossible to assert that megaspore formation is an essential part of the development. . . ."

An interesting feature noted in the Indian species is the fusion of the nuclei of the chalazal quartet followed by a degeneration of the fusion nucleus so that neither antipodals nor a lower polar nucleus are present.

Recently, Zweifel (1939), a pupil of A. Ernst, studied *B. abbreviata* and *B. indica*. In his account of the first species he says (p. 275): "Fast immer unterbleibt die Zellwandbildung nach der ersten und zweiten Teilung, und die vier frei im Plasma liegenden Kerne liefern durch eine weitere Teilung den achtkernigen Embryosack. Die Embryosackmutterzelle funktioniert also direkt als Makrospore. . . ." He does not deny the possibility of an Allium type of development, however, and says that in some cases the embryo sac arises from the upper dyad cell: "Eine einzige Teilung derselben (this means the megaspore mother cell) und Entstehung des Embryosacks aus der oberen Tochterzelle, wie sie von den genannten Forschern an *B. elongata* und *B. globosa* teilweise beobachtet wurde, und auch von Kuwada für *B. japonica* beschrieben wird, konnte ich in meinen Präparaten ebenfalls feststellen. Die erste Teilungsspindel der Makrosporenmutterzelle liegt dann immer an der Zellbasis und von den gebildeten beiden Zellen wird die kleinere basale bald verdrängt. Solche Zellteilungen liegen in meinen Präparaten aber nur äusserst selten vor."

Unlike the conditions described for *B. dioica* (Ekambaram and Panje, 1935), Zweifel notes that in *B. abbreviata* the nuclei at the antipodal end of the embryo sac do not fuse or degenerate but remain in a healthy condition and may even undergo some further divisions so that sometimes as many as six nuclei are seen in this region. One of these moves up and fuses with the upper polar nucleus.

In *B. indica*, too, Zweifel found an Adoxa type of embryo sac, but here again deviations were noted and the author draws two figures to show the possibility of tetrad formation. In these the lower dyad cell has divided

anticlinally to form two megaspores, but in the upper, which is considerably larger, there is no wall separating the two nuclei. The author states however that a wall is to be laid down later and eventually the uppermost cell will give rise to the embryo sac. Here then, the development would correspond to the Normal type as described for *B. dioica* by Ekambaram & Panje (1935).

The latest contribution (Fagerlind, 1945) deals with *B. elongata*. He shows very clearly that the first as well as the second reduction division is followed by wall formation (cf. *B. dioica*, investigated by Ekambaram & Panje) resulting in a normal tetrad of megaspores. The micropylar megaspore is the largest; the three chalazal ones are small and not always easily distinguishable from the adjacent somatic cells. It appears that due to this difficulty previous workers were led to erroneous interpretations of the development of the *Balanophora* embryo sac. It seems fairly certain now that no species of this genus belongs to the Adoxa type and probably none even to the Allium type. A reinvestigation of *B. abbreviata* and *B. indica* would be welcome but the likelihood is that these will be found to have embryo sacs of the monosporic type.

*Rhopalocnemis.*—Lotsy (1901), who studied *R. phalloides*, considered the development to be of the Adoxa type. As Fagerlind (1938, p. 468) remarks, however, it is more likely that it is of the Allium type, similar to *Helosis*. A reinvestigation is desirable.

### Hydnoraceae

Dastur (1922) reported Adoxa type in *Hydnora africana*. Fagerlind (1938, p. 470) has discussed this case in sufficient detail and I am in agreement with his view that Dastur's interpretation is incorrect (see also Maheshwari, 1937, p. 396). It is more likely that the development is of the Normal or the Allium type. A reinvestigation is desirable.

### Aizoaceae

In a paper dealing chiefly with the morphology and anatomy of *Mesembryanthemum pseudotruncatellum*, Schmid (1925) says that the embryo sac arises directly from the megaspore mother cell. He gives no figures to support this statement however, and it seems certain that this is a hasty conclusion (see also Fagerlind, 1938, p. 469; 1939, p. 14). Other plants of the family have a monosporic eight-nucleate embryo sac.

### Caryophyllaceae

Gibbs (1907) reported that in *Stellaria media* the embryo sac develops according to the Adoxa type. Rocén (1927), who made a comparative study of several members of the family Caryophyllaceae and the order Centrospermales in general, criticized this observation and regarded the embryo

sac as normal. P. C. Joshi (1936) renewed this controversy by saying that the further development of the megaspore mother cell was "variable." He reports that he never came across a row of three or four megaspores and only in a few cases did he see the mother cell give rise to two superposed cells with a transverse or oblique wall between them. This would give the impression that the development is usually of the Adoxa type but sometimes of the Allium type. Joshi does not seem to be quite certain however and confuses the issue by adding that "this does not preclude the possibility that the two megaspores[10] may give rise to three or four megaspores."

In reviewing this work some years ago (Maheshwari 1937, p. 394), I suggested that the row of three cells shown in his figure 35 and the four cells arranged in the form of a 'T' in figure 36 indicated that the embryo sac is monosporic.

Since then Fagerlind (1939, p. 14) has also commented on P. C. Joshi's observations and agrees with me that the latter's interpretation of the occurrence of the Adoxa type in this species is "äusserst unbefriedigend" and that "irgendwelche Gründe dafür bei *Stellaria media* an eine Entwicklung nach dem *Adoxa*-Schema zu glauben, liegen demnach nicht vor."

## Capparidaceae

A remarkable anomaly has been reported by Billings (1937) in *Isomeris arborea*, a xerophytic plant, collected from the Colorado and Mohave deserts, California. There is a tendency towards degeneration in the anthers as well as ovaries and only a small proportion of the flowers set fruit.

The first division of the hypodermal archesporial cell is periclinal, "resulting in an outer parietal and an inner sporogenous cell." "The primary parietal cell now initiates a series of periclinal divisions by which daughter cells are formed that overlie the sporogenous cell by a group from two to six cells in thickness, though the prevailing number, by far, is 3."

"An examination of much material in the sporogenous cell stage, and following, plainly indicates that the cell typically develops directly into the embryo sac without the formation of megaspores. A single instance was observed, however, in which they were present, and their position and appearance was quite in accord with what would have been expected in such an instance."

In the majority of cases the first division of the megaspore mother cell is said to give rise to the binucleate stage, in which the two nuclei are always separated by a central vacuole. In the next stage the primary micropylar nucleus alone divides and we thus get a three-nucleate stage after which as a rule there are no further divisions. "The typical definitive embryo sac in *I. arborea* has three nuclei which are organized into what seems

[10] These must be the dyad cells.

to be an egg apparatus. The two upper, of pyriform shape with their associated cytoplasm, resemble synergids and are doubtless truly such. The lower nucleus may appear like an egg but perhaps more like an endosperm nucleus. There is a complete absence of polar nuclei and antipodals." The author tries to compare the embryo sac of *Isomeris* with that of *Plumbagella* (as originally described by Dahlgren, 1916) but concludes that "the embryo sac of this species (i.e., *Isomeris arborea*) doubtless belongs to an entirely new type, as it does not find a parallel in any listed by Schnarf (1929) nor in the literature issued since the publication of his book."

Regarding later stages, the author summarizes the situation in the following words (p. 325): "A pollen tube may enter the micropyle and form a bulbous terminus in the embryo sac. It does not discharge its contents, but instead develops a thickened wall and remains intact during the earlier stages of endosperm development. The synergids generally disintegrate at the beginning of endosperm development, but one of a pair occasionally continues activity, becomes richly protoplasmic, and by cell division forms a cell row that extends a short distance downward from the micropylar end of the embryo sac. This activity seems to serve no important useful purpose. Endosperm begins as a free-cell formation but afterwards exhibits two definite types of structure, a nodular type consisting of circumscribed masses of coarsely granular cytoplasm containing free nuclei; a cellular type consisting of vacuolated cells in the form of a tissue. The nodular type does not extend into the short arm of the J-shaped embryo sac. The embryo arises by a direct outgrowth of an endosperm nodule which is generally located near the base of the convex curve of the sac. In one instance an embryo was found developing from a nodule in the micropylar region."

Five years ago (Maheshwari, 1941, p. 223) I commented upon this account as follows: "Several of the above statements appear to be of a doubtful nature. To mention a few instances, fig. 19 which would ordinarily be interpreted as a clear tetrad of megaspores of which the lowest is dividing, is regarded by him as showing 3 wall cells and an embryo-sac mother cell. Similarly fig. 18 in which the axial row clearly consists of one wall cell and 4 megaspores, of which the lowest has enlarged, is regarded as composed of 4 parietal cells and 'a vacuolated sporogenous cell.' Various other ingenious interpretations have been offered which cannot be considered here in detail. It is sufficient to state that the illustrations entirely fail to support the conclusions based upon them."

My recent study of the work of Billings makes me feel even more doubtful than I did previously about the validity of his conclusions. So far as the development of the embryo sac is concerned I would interpret it as of the usual monosporic type although the frequent occurrence of degenerations may at times obscure the real picture. The post-fertilization stages

need careful study to see whether the embryo arises from the egg (as is more probable) or from the endosperm.[11] It would also be of interest to compare the behavior of *I. arborea* with that of the other species belonging to this genus.

### CRASSULACEAE

D'Hubert (1896) considered the embryo sac of *Sedum* to be of the Adoxa type. He said: "La cellule mère donne directement le sac embryonnaire." Mauritzon (1933) has shown, however, that it is of the Normal type.

### SAXIFRAGACEAE

Elst (1909) reported Adoxa type in *Philadelphis coronarius*. Gäumann (1919) and Mauritzon (1933, p. 109) have found this to be incorrect. Tetrad formation occurs normally and the development is of the Normal type.

### LEGUMINOSAE

Guignard (1881) in *Medicago arborea* and *Lupinus polyphyllus*, and Young (1905) in *Melilotus alba*, considered the development to be of the Adoxa type, but this is certainly incorrect. Reeves (1930), Cooper (1936), and Farley and Hutchinson (1941) have shown that it is of the Normal type in *Medicago:* and the same is true of *Melilotus* (Cooper, 1933). In a recent paper Markowa (1944) states that in the tribe Vicieae the genus *Cicer* is an exception, having an embryo sac of the Adoxa type and a long and cellular suspensor, and that it should therefore be placed in a new tribe Intermediae, between the Trifolieae and Genisteae. The author does not give any convincing illustrations, however, to support the occurrence of the Adoxa type in *Cicer* and it seems likely that on reinvestigation this will be found to have a Normal type of embryo sac as in the other Leguminosae.

### RUTACEAE

Mauritzon (1935) stated that in *Xanthoxylum* spp. the development could be of the Normal, Allium or Adoxa types. As Fagerlind (1939) points out, the peculiar appearances seen by him are no doubt due to the occurrence of apospory and it is surprising that Mauritzon did not take this possibility into consideration. Fagerlind concludes: "Das *Adoxa*-Schema liegt kaum hier vor."

### EUPHORBIACEAE

Modilewski (1910) investigated the embryo sac of *Euphorbia hetero-*

[11] Tischler (1943, pl 617) comments as follows: "Die Angabe von Billings (1937), dass die Capparidacee *Isomeris arborea* haploidparthenogenetisch sei und dass der Embryo aus dem unbefruchteten Endosperm entsteht, ist, so lange keine Bestätigung von anderer Seite vorliegt, m. E. völlig unglaubwürdig."

*phylla* and reported a Normal type of embryo sac in this and several other species of the genus. Sanchez (1938), on the other hand, found in *E. heterophylla* an Adoxa type of embryo sac. Since his figures and descriptions were not very convincing, I was prompted to reinvestigate it (Maheshwari, 1942) and can definitely say that the development is not of the Adoxa type but of the Normal type as originally reported by Modilewski.

### Limnanthaceae

The embryo sac of *Limnanthes douglasii* has been investigated by four different workers but without any complete agreement regarding the exact mode of its development. Leaving aside Hofmeister's (1858) work, which was done with free hand sections, we come to Stenar (1925a), who reported an Adoxa type of embryo sac in this plant but noted the reduction in size of the chalazal nuclei of the embryo sac. Following him, Eysel (1937) investigated some material of the same species, obtained from the Botanical Gardens of the Universities of Marburg, Bonn and Edinburgh, and confirmed Stenar's observations in most respects. He found however an occasional reduction in the number of nuclei at the chalazal end of the embryo sac owing to a failure of the lowest nucleus of the four-nucleate stage to undergo the last division. An interesting observation made by him is the frequent disappearance of the wall separating the megaspore mother cell from the nucellar cell situated directly below it and the subsequent incorporation of the latter into the embryo sac. One embryo sac showed nine nuclei, seven of which had organized into cells at the micropylar end of the embryo sac (four looking like synergids; two looking like egg cells; two 'polar' nuclei; and the nature of one cell remained undecided). No antipodal cells or nuclei were seen in this case.

Fagerlind (1939) had apparently no knowledge of Eysel's work as he does not refer to it in his paper. His material, which was collected in the Botanical Gardens, Stockholm, has been interpreted differently. The first division of the megaspore mother cell gives rise to two nuclei which become separated by a large vacuole. The lower of these usually degenerates right away and forms just a densely staining homogeneous blob which lies close to the bottom of the embryo sac and takes no part in further development. The upper nucleus now divides to give rise to two nuclei of which the lower (this will be designated hereafter as the middle nucleus) has the same fate as the primary chalazal nucleus mentioned above. After the meiotic divisions are over, we thus have a three-nucleate stage in which the micropylar nucleus alone retains the capability of further division. This gives rise to a quartet which produces the egg apparatus and a polar nucleus. Of the two degenerating nuclei, one may be considered as an antipodal and the other as the lower polar.

There are other methods of development, however. After the three-

nucleate stage arising as a result of the meiotic divisions, the uppermost nucleus alone divides in the next stage. The middle one does not degenerate, however, as in the first case but remains quiescent for a time and reawakes to take part in the fourth division. We thus come to have a seven-nucleate embryo sac in this instance with two antipodals instead of one.

A further step in the "gesteigerte Vitalität" of the nuclei is seen when the middle nucleus of the three-nucleate stage divides synchronously with the micropylar nucleus, but only one of its daughter nuclei divides again with the result that this time the embryo sac is eight-nucleate.

Still other variations are mentioned by Fagerlind (1939) and the diagram given by him on page 27 of his paper seems to include all the possibilities that one can think of. The multiplicity of these variations nevertheless calls for a further study of this plant, based on material collected from its native habitat. It may be that at least some of these abnormalities are due to greenhouse or garden conditions. Eysel's work does not mention the possibilities visualized by Fagerlind, and the latter in his turn does not consider the possibility of the incorporation of a nucellar cell into the embryo sac as noted and figured by Eysel.

It seems difficult for the present to assign *Limnanthes* to any of the usual types of embryo sac development. According to Fagerlind (1939) the egg apparatus is separated from the megaspore mother cell stage by four nuclear divisions and not three, and if this is correct, the development is not of the Adoxa type where only three nuclear divisions intervene between the megaspore mother cell and the egg.

### Theaceae

Cavara (1899) stated that in *Thea sinensis* the development is of the Normal type and the embryo sac arises from the micropylar megaspore, whereas Cohen-Stuart (1916) believed it to be of the *Adoxa* type. Fagerlind (1939, p. 17) finds both of them to be wrong; the embryo sac is of the Allium type.

### Tamaricaceae

The genus *Tamarix* has already been dealt with on page 78. Frisendahl (1912) reported an Adoxa type of embryo sac in *Myricaria germanica*, but his figures, which are remarkably clear and faithful, gave good indications that the development was really of the Fritillaria type (see Schnarf, 1931, p. 94). Zabban (1936) actually proved it by demonstrating the chalazal fusions and the triploid nature of the nuclei in the chalazal half of the embryo sac. Battaglia (1942) has confirmed this.

### Caricaceae

Heilborn (1921, 1928) reported that in *Carica papaya* and some other

species of this genus, wall formation does not occur during megasporogenesis and that all four megaspore nuclei lie free in the mother cell. Only one nucleus at the micropylar end now divides again so that the mature embryo sac is five-nucleate. His results are however at variance with those of other workers. Agharkar & Banerji (1930), who investigated some material of *Carica papaya* from India, find that tetrad formation takes place in the usual way and the mature embryo sac is eight-nucleate. They conclude that "it is not possible to account for his (Heilborn's) results except on the supposition that the Equadorian species of *Carica* differ from the rest in their gametophytic development." More recently, Fagerlind (1939) and L. T. Foster (1943) have also observed a Normal type of embryo sac and Heilborn's supposition that *C. papaya*, being a cultivated plant, has several races behaving differently, no longer seems plausible. There is hardly any doubt now that the other species investigated by him (*C. candamercensis*, *C. chrysopetala* and *C. pentagona*) and reported to have tetrasporic embryo sacs of the Adoxa type will also turn out to be normal.

Mention may also be made here of the contributions of Usteri (1907) and Kratzer (1917). These authors agree that the embryo sac is monosporic and eight-nucleate. But while Usteri thought it was the micropylar megaspore which gave rise to the embryo sac, Kratzer is less sure of that point. He writes (p. 306): "Ebenso wird nicht immer dieselbe Zelle zum Embryosack. Ich konnte unzweideutig feststellen, wie sich bald die oberste, bald die unterste dazu entwickelt."

### Cactaceae

D'Hubert (1896) considered the embryo sac of *Phyllocactus* sp. to be of the Adoxa type. He says: "Quand l'ovule est complètement developpé, la cellule sous-épidermique donne le sac embryonnaire par 3 bipartitions successives de son noyau. Le sac embryonnaire provient donc directement de la cellule sous-épidermique axile du nucelle." The central vacuole seen by him at the two-nucleate stage, coupled with the fact that other Cactaceae so far studied (see Mauritzon, 1934; Neumann, 1935) have a normal type of embryo sac, make it seem fairly certain however that he was wrong in his interpretation. Further work on the embryology of this family would of course be welcome as it has not received adequate attention in this respect.

### Myrtaceae

Pijl (1934) reported a five-nucleate embryo sac in *Eugenia jambos* and *E. bancana*. After reduction division, only the micropylar megaspore nucleus divided again and gave rise to the egg and one synergid, the second micropylar nucleus functioned directly as a synergid, and the two chalazal nuclei as the polars. His figures, which are entirely diagrammatic, are quite

inadequate to substantiate this story and it seems likely that a reinvestigation of *Eugenia* will show the occurrence of a monosporic eight-nucleate embryo sac with the possible difference that the antipodals may be of an ephemeral nature.

### HYDROCARYACEAE

Gibelli and Ferrero (1891) reported an embryo sac of the Adoxa type in *Trapa natans*, but Ishikawa (1918) saw regular tetrad formation in this species and Maheshwari (unpublished) has confirmed it in *T. bispinosa*. There is no doubt therefore that the development is of the Normal type. Fagerlind (1939, p. 20) also writes: "Hier liegt sicher der Normal-typ vor. Diese Auffassung wird durch Maheshwaris Nachweis dieser Entwicklungsart bei *Trapa bispinosa* bekräftigt."

### PLUMBAGINACEAE

Dahlgren (1916) had reported Adoxa type in *Armeria alpina*, *A. plantagineae*, *A. vulgaris*, *Statice bahusiensis*, *S. gmelini* and *S. macroptera*. Subsequent work has shown however that in *Armeria* the development is of the Fritillaria type (Fagerlind, 1939a; D'Amato, 1940a), and in *Statice* some species follow the Fritillaria type and others the Penaea type (Fagerlind, 1938, 1939a).

### OLEACEAE

Billings (1901) wrongly interpreted the embryo sac of *Forsythia suspensa* to be of Adoxa type. Andersson (1931, p. 52) showed that the development is normal.

### FOUQUIERIACEAE

Johansen (1936) reported a peculiar type of development in three species of *Fouquieria: F. splendens*, *F. peninsularis*, and *F. burragei*. According to this account the embryo sacs are tetrasporic but may have eight, six, or only five nuclei. Mauritzon (1936), who made an independent study of *F. splendens*, found a Normal type of embryo sac. Johansen (1936) seems to have missed some stages between his figs. 1 and 2 of *F. splendens* (see Fagerlind, 1939, p. 15; and Khan, 1943).

### SOLANACEAE

Nanetti (1912) reported that the development of the embryo sac in *Solanum muricatum* followed the "tulip" type. He saw nothing to indicate the formation of a tetrad of megaspores nor did he note any degenerating megaspores on top of the young embryo sac. Young (1923, p. 330), who studied *S. tuberosum*, also made a vague statement saying that the archesporial cell grows rapidly and "at this stage it may be regarded as a megaspore; further development is delayed for a time." Elsewhere he says: "In

a few instances a row of two or three sporogenous cells was found in the axis of the ovule, suggesting a transverse division of the original archesporial cell, though it is apparent that this is not the ordinary method of megaspore formation."

Since then, Rees-Leonard (1935) and Lamm (1937) have shown that *S. tuberosum* follows the Normal type and there is no doubt that *S. muricatum*, like other species of this genus (Krüger, 1932; Bhaduri, 1932) will be found to be similar.

### Gesneriaceae

Cook (1907, p. 180) makes a very brief statement on the development of the embryo sac in *Rhytidophyllum crenulatum* and *R. tomentosum:* "The single archesporial cell elongates without division, in the antipolar direction, the new part being smaller in diameter than the older part. This cell then elongates very rapidly, and forms the two- and four-nucleate stages of the embryo-sac. At this time the sac is usually about twice as long as wide. Without further enlargement of the sac the nuclei now divide, thus forming the eight-nucleate stage." From this one would conclude that the development is of the Adoxa type. The author noted one instance however in which the archesporial cell had divided into two 'megaspores.'[12] This and the fact that the two-nucleate stage (his fig. 5) shows prominent vacuolation make it difficult to lay much confidence in Cook's account and a reinvestigation is necessary. All other members of the Gesneriaceae, so far studied, have a Normal type of embryo sac.

### Acanthaceae

Karsten (1891), who investigated the embryo sac of *Acanthus ilicifolius*, stated that as far as he could ascertain the megaspore mother cell grew directly into the embryo sac without undergoing any cell divisions. Gigante (1929) has shown however that the development is of the normal type.

### Myoporaceae

In *Myoporum humile*, David (1938) has recently described a vacuolated megaspore mother cell which is said to give rise to a Lilium (=Adoxa) type of embryo sac. She writes (p. 681): "Da ich überdies nirgends Kappen über der Embryosackmutterzelle beobachtete, entwickelt sich hier der primäre Embryosack offenbar ohne vorherige Tetradenbildung (*Lilium-Typ*)." The considerable gap between her figs. 1 and 2, the presence of a distinct vacuolation at the uninucleate stage and the further appearance of a large central vacuole at the two- and four-nucleate stages leaves no doubt however that she entirely missed the stages in megasporogenesis and the embryo sac is really of the monosporic eight-nucleate type. Fagerlind (1939, p. 46) says: "Eine Nachuntersuchung ist notwendig."

[12] These must be the dyad cells.

### COMPOSITAE

Ward (1880) thought that the development of the embryo sac of *Pyrethrum balsaminatum* corresponded to the Adoxa type. Fagerlind (1939, figs. 10, 11) studied some specimens growing in the Stockholm Botanical Garden and made the observations summarized below.

As in other Compositae, the nucellus is of the reduced type. The archesporium is usually two-celled but sometimes three cells are seen and occasionally only one may be present. As a result of the first meiotic division, two nuclei are formed of which the uppermost soon increases in size as compared to the lower. Both of them undergo the second division and the resulting four nuclei take up a 1+3 arrangement. The micropylar nucleus is the largest and functions while the chalazal nuclei soon begin to degenerate. Vacuolation takes place at this stage and is followed by the appearance of a lateral bladder-shaped outgrowth which assumes a tubular form and gradually makes its way upwards into the micropyle. The functioning megaspore nucleus, which has by this time moved into the apex of this tube, divides to form two nuclei and then four. The latter lie in two pairs, one at each end of a large vacuole. The next division gives rise to eight nuclei, of which the upper four form the egg apparatus and the upper polar nucleus, and the lower four the three antipodal cells and the lower polar nucleus. The lowest antipodal cell forms the connection between the 'bladder' and the body of the old megaspore mother cell in which the three degenerated megaspore nuclei are sometimes still distinguishable. The nuclei of the antipodal cells undergo some divisions but the daughter nuclei fuse once again to form a single lobed nucleus.

As Fagerlind points out, Ward seems to have completely overlooked the three degenerated megaspore nuclei and thus considered the development to be of the Adoxa type. It is now clear that five divisions actually take place, between the megaspore mother cell and the mature embryo sac, as in the Normal type.

### TYPHACEAE

Schaffner (1897) reported that in *Typha latifolia* "the macrospore mother cell develops directly into the fertile macrospore without any division," i.e., the embryo sac is tetrasporic. But Dahlgren (1918) demonstrated that megaspore formation takes place normally and the chalazal cell of the tetrad functions to give rise to an eight-nucleate embryo sac.

### ALISMACEAE

All members of this family so far investigated have been shown to have an embryo sac of the Allium type with a tendency towards some reduction in the chalazal end.

*Alisma.*—Ward (1880), who was the first to investigate *A. plantago*,

claimed that the megaspore mother cell divides into two cells, of which the upper divides once, but the daughter cells thus formed quickly degenerate. The nucleus of the lower cell divides thrice to give rise to the embryo sac. In the same year Fischer noted that the upper cell remains undivided and soon degenerates while the lower behaves as described by Ward. Schaffner (1896) interpreted the degenerating cell as a parietal cell and thought the development was of the Adoxa type. Sometimes he saw only two nuclei (instead of four) at the chalazal end of the embryo sac but believed that he had perhaps missed the others. Nitschke (1914) disagreed with all of these workers and reported that the megaspore mother cell produced four free nuclei, three of which were cut off at the top by a wall while the remaining nucleus divided thrice to give rise to the embryo sac. According to him the development is therefore of the Normal type. The correct interpretation was finally given by Dahlgren (1928) who showed clearly that there is a hypodermal megaspore mother cell which divides into two dyad cells, of which the lower gives rise to the embryo sac. Since the two chalazal nuclei of the four-nucleate stage do not undergo further division, the mature embryo sacs are six-nucleate. Of the two nuclei at the chalazal end, one functions as an antipodal and the other as a lower polar nucleus. Johri (1936b) confirmed Dahlgren's account and found another species, *A. plantago-aquatica*, to behave similarly. He noted however that in certain cases the chalazal nuclei were able to complete the last division and the embryo sacs could occasionally have more than six nuclei.

*Sagittaria*.—Schaffner (1897) investigated *S. variabilis* and reported the embryo sac to be eight-nucleate but was unable to follow the earlier development. A few years later, Cook (1907), working on *S. lancifolia*, wrote that it was similar to *S. variabilis* but that the antipodals were ephemeral. Dahlgren (1934) traced the whole development in *S. sagittifolia* and showed that the embryo sac arises from the lower dyad cell and is therefore bisporic. This was confirmed by Johri (1935a & b; 1936b) for this, as well as three other species, viz., *S. guayanensis*, *S. latifolia* and *S. graminea*, although he found that occasionally seven- or eight-nucleate embryo sacs are also formed as in *Alisma*.

### Butomaceae

Hall (1902) investigated *Limnocharis flava* (now *L. emarginata*) and reported the development to be of the Adoxa type. On the other hand, Nitschke (1914) claimed that the embryo sac was formed from the third megaspore of a T-shaped tetrad. Johri (1938) showed however that the development is really of the Allium type, the embryo sac arising from the lower dyad cell. After the two-nucleate stage the primary chalazal nucleus quickly degenerates and is cut off by a thin membrane from the rest of the embryo sac. The primary micropylar nucleus divides twice and

produces the egg apparatus and upper polar nucleus. The mature embryo sac is thus usually five-nucleate but occasionally the primary chalazal nucleus may divide or undergo fragmentation resulting in six-, seven-, or even eight-nucleate embryo sacs. It now appears that Hall misinterpreted the upper dyad cell as the primary parietal cell.

### GRAMINEAE

Miller (1919) thought that all four megaspore nuclei enter into the formation of the embryo sac of *Zea mays*, so that the development is of the Adoxa type. Weatherwax (1919) and Cooper (1937) have shown that a tetrad of megaspores is formed as usual and the lower of these functions to give rise to an eight-nucleate embryo sac.

### PALMAE

*Cocos*.—Working on *C. nucifera*, Quisumbing and Juliano (1927) write: "The nucleus of the megaspore mother cell of the embryo sac next divides into two, more or less unequal in size, without wall formation. . . . In the coco palm the formation of the tapetal cell and the four megaspores is eliminated, the two daughter nuclei lying side by side." It seems, however, that the authors missed all stages of megasporogenesis. The chromosome condition of the two nuclei in fig. 9 appears to indicate that they are the nuclei of two megaspore mother cells lying obliquely oriented with respect to each other so that the separating wall was entirely overlooked. Besides, the two nuclei are quite equal and similar and not "unequal" as stated in the text. In an earlier paper, Bauch (1911) mentions the occasional occurrence of two megaspore mother cells and he also noted the presence of degenerating megaspores. It seems very likely therefore that the embryo sac of *Cocos* is of the Normal type. A reinvestigation is desirable.

*Chamaerops*.—In *C. humilis*, Gioelli (1930) reported a modified Adoxa type. According to his statements there is no wall formation after the first division of the megaspore mother cell and the two nuclei move apart to the opposite poles. Only the micropylar divides again, first to form two, and then four nuclei, the chalazal nucleus remaining undivided. The mature embryo sac is thus five-nucleate. Gioelli's figures and descriptions are however so unsatisfactory that little reliance can be placed on his observations. In his fig. 3 he shows a large central vacuole at the two-nucleate stage, which would indicate that the development is not of the Adoxa type but of the Normal type.

### ARACEAE

*Homalonema*.—In a contribution dealing with the embryology of 11 aroids, none of which however seems to have been satisfactorily investi-

gated, Gow (1913) states that in *Homalonema argentea* the primary archesporial cell "divides once transversely, and of the two resultant cells the outer one functions, the inner one being broken down and absorbed." The author says that "whether the latter is to be regarded as one of a 'row of two' or as a vestigial tapetum is purely an academic question." He thus attached no importance whatever to the morphological nature of these cells nor does he mention the intervening stages leading to the eight-nucleate embryo sac. The plant needs a fresh study.

*Richardia*.—Gow (1913, p. 136) is less vague though not more correct in his account of *Richardia africana* and says: "No primary parietal cell is formed. The primary archesporial cell is in this species, the spore mother cell, and develops directly into an embryo sac without the previous formation of a row of megaspores." The two- and four-nucleate stages figured by him nevertheless show the vacuolation characteristic of a monosporic embryo sac and Michell (1916) has actually demonstrated that a tetrad of megaspores *is* formed. According to her "in no case is there anything to lead one to suppose that the embryo sac has originated directly from the megaspore mother cell."

*Aglaonema*.—Gow's (1908) work on *A. versicolor* is of such a fragmentary nature that it is mentioned here only for the sake of completeness. He was unable to trace the precise development and showed only a two-nucleate and a four-nucleate stage of the embryo sac.

In a paper entitled "The embryo sac of *Aglaonema*," Campbell (1912) states that in *A. simplex* and *A. modestum*, investigated by him, the four megaspore nuclei were not separated by walls; after this stage only one of the micropylar nuclei divided again and this division gave rise to the two synergids; the second undivided nucleus functioned as the egg and the two chalazal nuclei as the polars. This would seem to indicate that one of the megaspore nuclei functioned directly as the egg and two as the polars —a condition once reported in *Plumbagella* but now proved to be incorrect.

Apart from the unsatisafctory nature of Campbell's observations, none of the Araceae so far investigated (see Jüssen, 1928) has been found to have a tetrasporic embryo sac. Fagerlind (1939, p. 44) remarks briefly and well: "Diese Angabe, die wohl als falsch anzusehen ist, hat kaum jemals Glauben gefunden."

All of Campbell's material was collected from plants growing under more or less artificial conditions and it may be well to reinvestigate the embryo sac of *Aglaonema* from material collected in its natural habitat.

*Acorus*.—Although Mücke (1908) reported the embryo sac to be of the Adoxa type, Jüssen (1928) and Buell (1938) have shown that it is really of the Normal type.

*Anthurium*.—Campbell's (1905) account of *A. violaceum* var. *leucocar-*

*pum* is unsatisfactory in several respects. In 1937, I remarked: "Needs reinvestigation." Fagerlind (1939) concurs with this view and says: "Der *Adoxa*-Typ ist hier wenig wahrscheinlich."

### LEMNACEAE

According to Caldwell (1899, p. 57), in *Lemna minor*, "the primary sporogenous cell seems to develop directly into the megaspore, and as such undergoes a long period of rest." A careful study of his figures seems to indicate however that he missed several stages in the early development of the embryo sac. A reinvestigation is desirable in view of the fact that *L. trisulca* (Jönsson, 1879/80) and *Wolffia arrhiza* (Gupta, 1935) have embryo sacs of the Allium type.

### COMMELINACEAE

In a recent study of the development of the embryo sac in *Commelina angustifolia*, McCollum (1939) remarks: "It seems quite certain that all the four nuclei resulting from the meiotic divisions of the megaspore mother cell, enter into the structure of the embryo sac. The lack of any evidence of walls separating the nuclei, also the lack of any evidence of disintegration of any of these nuclei points definitely to the same conclusion."

In spite of this categorical statement, McCollum's figures seem to indicate that he missed all stages in megasporogenesis and his interpretations are therefore incorrect.

In another species of the genus, *C. benghalensis*, investigated by Maheshwari & Singh (1934), the embryo sac is monosporic and eight-nucleate.

### CYNASTRACEAE

According to C. E. Fries (1919) the embryo sac of *Cynastrum johnstonii* is of the Adoxa type, but this is certainly incorrect, since the two- and four-nucleate stages show the central vacuole characteristic of monosporic embryo sacs. Stenar (1937) and Nietsch (1940) have demonstrated the Normal type.

### LILIACEAE

*Aloe*.—Several species of this genus (*A. arborescens*, *A. caesia*, *A. ciliaris*, *A. todari* var. *praecox* and *A. varvari*) were investigated by Gioelli (1930a) who reported that the development was of the Adoxa type. This was criticized by Maheshwari (1937), who interpreted Gioelli's fig. 9 of *A. caesia*, supposedly showing a four-nucleate embryo sac, as a T-shaped tetrad of megaspores. Joshi (1937), and Schnarf and Wunderlich (1939), have shown since then that megaspore formation takes place as usual and the embryo sacs are monosporic and eight-nucleate.

*Camassia*.—Leffingwell (1930) figured a few stages in the development of *C. quamash* and concluded that the development is of the Adoxa type. However, the large central vacuole seen at the two-nucleate stage did not support this interpretation and Fagerlind (1941) has actually shown that in this species as well as in *C. esculenta* and two other undetermined ones the development is of the monosporic eight-nucleate type. F. H. Smith (1942) has done the same for *C. leichtlinii*.

*Convallaria*.—One species of this genus, *C. majalis*, has attracted much interest. Wiegand (1900) reported that the first division of the megaspore mother cell gives rise to two dyad cells of which the outer is the larger. The next division is not accompanied by wall formation. Instead, the four nuclei, two in each cell, divide simultaneously, and as the partition wall between the upper and lower quartets breaks down, the development may be designated as of the Adoxa type.

Schniewind-Thies (1901), on the other hand, reported that the megaspore mother cell produced a row of four cells, only one of which functioned to produce the embryo sac while the remaining three degenerated, i.e., the embryo sac is of the monosporic type.

Stenar (1941) has reinvestigated the problem, basing his studies on material fixed from plants growing in their natural habitat. He has shown that the first division of the megaspore mother cell is followed by wall formation and results in the formation of two dyad cells, but the walls laid down after the second division are very thin and ephemeral so that we once again get the original dyad cells each of which contains two nuclei. The micropylar dyad cell is at first larger and more vacuolated than the chalazal, but gradually the latter increases in size and acquires the more dominant position. The two nuclei of this cell divide to form four and then the eight nuclei of the mature embryo sac. The development is therefore of the Allium type, the interesting point being that it starts like a monosporic form but is actually bisporic due to the early dissolution of the cell walls in the dyad cells.

*Fritillaria*.—As mentioned in the introductory part of this review, *Fritillaria* and *Lilium* were originally supposed to have an Adoxa type of embryo sac. Investigations carried out during recent years by Bambacioni (1928, a, b) and Cooper (1935) have shown that both these genera have an entirely different type of embryo sac in which four divisions take place between the megaspore mother cell stage and the formation of the eight-nucleate embryo sac.

*Gagea*.—Stenar (1927) reported Adoxa type in *G. lutea*. Since then several species of this genus have been shown to follow the Fritillaria type (Romanov, 1936) and it seems probable that *G. lutea* will be found to be similar. Fagerlind (1939, p. 39) says: "Der Fritillaria-Typ kann hier als so gut wie sicher festgestellt betrachtet werden." Of course, in exceptional cases all

four megaspore nuclei may divide just once to produce an eight-nucleate embryo sac of the Adoxa type as noted even by Romanov (1936) in *G. graminifolia*.

*Medeola*. McAllister (1909) reported Adoxa type in *M. virginica* but as I pointed out previously (Maheshwari, 1937) his figs. 40 and 41 of the four-nucleate stage show a marked difference of size between the micropylar and chalazal nuclei and indicate that the Fritillaria type is more likely. Fagerlind (1938, p. 483; 1939, p. 38) is in agreement with this opinion.

*Majanthemum*. McAllister (1914, p. 140) found that in *M. canadense* the first and second divisions of the megaspore mother cell are followed by the formation of cell membranes resulting in four fully separated cells which may be arranged either in an axial row, or, more frequently, in a more or less bilateral fashion. Later the partition membranes degenerate, thus giving rise to a tetranucleate cell whose nuclei undergo one further division to form the eight-nucleate embryo sac. Stenar (1934) has shown that in *M. bifolium* the embryo sacs are 16-nucleate (Drusa type) although they may appear eight-nucleate in later stages owing to an early degeneration of some of the antipodals. *M. canadense* thus needs to be reinvestigated.

*Smilacina*. McAllister (1909, 1914) investigated several species of this genus. He reports that in *S. sessilifolia* and *S. stellata* the four nuclei resulting from the first two divisions of the megaspore mother cells are at first separated by cell membranes but they soon disappear and the development takes the course laid down for the Adoxa type. Stenar (1934) suspects that they would turn out to be similar to *Majanthemum*. Fagerlind (1938, p. 483; 1939, p. 38) is in agreement with this view. A reinvestigation is necessary to determine whether the development is of the type seen in *Majanthemum* or *Fritillaria*.

*Tulipa*. Early reports (Ernst, 1901; Guignard, 1900; Newton, 1927) of the occurrence of the Adoxa type in several species of this genus are now regarded as doubtful in the light of the investigations made by Bambacioni-Mezzetti (1931) and Bambacioni and Giombini (1930). The Adoxa type does not occur in any of the species belonging to the section Leptostemones. A modified Adoxa type, noted in members of the section Eriostemones, has already been described on page 76.

## AMARYLLIDACEAE

*Amaryllis, Buphane, Nerine*. Schlimbach's report (1924) on *Amaryllis belladonna*, *Buphane disticha* and *Nerine curvifolia* is extremely brief and unillustrated. All of these plants should be reinvestigated.

*Cooperia*. Church (1916), working on *C. drummondii*, says: "Megaspore formation takes place in the way usual for the Liliaceae. The archesporial cell becomes directly the one-celled stage of the embryo sac." She com-

pares her observations with those of Treub and Mellink (1880) on *Lilium* and *Tulipa*, and of Schaffner (1901) on *Erythronium* and concludes: "We may for the present assume that the reduction division occurs with the division of the one-celled stage and is completed when the four-nucleate embryo sac is formed." A study of her figs. 3 and 4 seems to indicate however that she missed several stages between the megaspore mother cell and the two-nucleate embryo sac. A reinvestigation will probably show that the embryo sac is not of the Adoxa type but of the Normal type.

*Crinum*.—Schlimbach (1924) reported Adoxa type in *C. asiaticum* without offering any illustrations to support his statement. On the other hand, Stenar (1924) and Tomita (1931) found Allium type in certain species of this genus. The latter condition seems more likely, but a reinvestigation is necessary.

*Cyrtanthus*.—Farrell (1914), who investigated "the ovary and embryo of *C. sanguineus*," does not figure any stages in embryo sac development but merely writes that "some of the ovules which were killed in the early stages were examined and found to contain an embryo sac of the lily type." Stiffler (1925), working on *C. parviflorus*, supports this statement and states (p. 212): "The product of the heterotypic division is the 2-nucleate embryo sac with a large vacuole in the center between the nuclei. . . . The homotypic division forms the four-nucleate stage, with two nuclei occupying each end of the sac." The fact that a large central vacuole is seen at the two- and four-nucleate stages, together with certain other considerations, makes it almost certain that these investigators were mistaken and the development is really of the Normal type (see also Fagerlind, 1938, p. 484; 1939, p. 39).

*Haemanthus*. –Schlimbach (1924) and Stenar (1925) found that in *H. catharinae* the development of the embryo sac corresponded to the Normal type. Woycicki (1928), on the other hand, considered it to be of the Adoxa type. As Fagerlind (1938, p. 484) points out, the presence of a large central vacuole at the two-nucleate stage indicates that the earlier observations of Schlimbach and Stenar are more likely to be correct. In a later paper (Fagerlind, 1939, p. 39) he says: "Der Normal-Typ ist hier so gut wie sicher" and I am in agreement with this opinion.

## Zingiberaceae

Humphrey (1896, p. 22) writes of a species of *Costus:* "The mother cell of the embryo sac enlarges as the ovule grows but does not divide further and thus becomes itself the definitive embryo sac." This is supported by Mauritzon (1936, p. 28) who states: "Ich habe viel Zeit darauf verwendet, die Embryosackentwicklung bei *Costus igneus* zu studieren and hierbei meine Präparate nur in der Weise deuten können, dass oben zitierte Darstellung auch ganz auf diese Art passt." He notes however that the

development does not entirely agree with that in other forms showing the *Adoxa* type, for in these vacuolation commences only after the megaspore nuclei have been formed. "Bei *Costus* dagegen wächst die junge Embryosackmutterzelle zuerst lange und wird vacuolisiert, bevor der Kern sich ohne darauf folgende Wandbildung teilt."

The irregular vacuolation observed by Mauritzon seems to indicate that he missed the stages in megasporogenesis and misinterpreted the functioning megaspore as the megaspore mother cell. Since then Banerji & Venkateswarlu (1936) have found a Normal type of embryo sac in *C. speciosus* and Fagerlind (1939) has done the same in *C. cylindricus*.

## Orchidaceae

*Epidendrum, Bletia.*—In *Epidendrum variegatum* and *Bletia shepherdii*, Sharp (1912) reports that, although the embryo sac usually develops according to the Normal type, sometimes wall formation between the megaspores is partially or completely absent and the embryo sacs may be bi- or tetrasporic. Since these differences are probably due to environmental factors, no great importance need be attached to this abnormality.

*Epipactus.*—In *E. pubescens*, according to Brown and Sharp (1911), "in most cases, the megaspore mother cell divides to two unequal daughter cells, the chalazal one again dividing to form two megaspores. The innermost megaspore then gives rise to the embryo sac." In certain other cases, however, "the fate of the megaspore mother cell is quite different." "After enlarging somewhat the nucleus divides, the spindle lying at about the center of the cell, so that the thin wall formed upon the fibers separates the mother cell into two nearly equal daughter cells. The wall, however, soon disappears, leaving the two nuclei in a single cell cavity which is to form the embryo sac. Between the nuclei vacuolation occurs, so that the center of the sac comes to be occupied by a single large vacuole, the two nuclei taking up positions at opposite ends of the sac, where the greater part of the cytoplasm lies." These nuclei are now said to form four and then eight, so that in such cases the development is to be considered as of the Adoxa type. While such a variation is possible, a reinvestigation of *Epipactis* would be useful.

*Gyrostachys.*—In 1914 Pace published a paper on two species of *Gyrostachys* (=*Spiranthes*) named *G. gracilis* and *G. cernua*. She says that "the embryo sac is very irregular in its development. Sometimes it develops from the mother cell, sometimes from the daughter cell (she evidently means a dyad cell) and at others from either of the megaspores. The sac may contain four, five, six or eight nuclei, the six-nucleate sac resulting from a lack of one mitosis in the chalazal end of the sac being the usual one in my material."

Pace's illustrations seem to convey the impression however that the

embryo sac is as a rule monosporic and not bi- or tetrasporic as she often believed it to be. The two-nucleate stage shown in her fig. 4 has such a large and typical central vacuole that its direct origin from the megaspore mother cell appears to be highly improbable. It seems more likely that she occasionally missed some of the degenerating megaspores and thus arrived at different interpretations. In an Indian species of *Spiranthes*, which I have investigated from material growing under natural conditions (observations unpublished) the embryo sac is clearly monosporic and I have found no evidence of its being occasionally bi- or tetrasporic.

The four-nucleate condition of the embryo sac, reported by Pace in certain instances, is also doubtful. As she herself admits (p. 10), this condition "may be due to the decay of some of the chalazal nuclei." The other alternative of course is that she missed some of the chalazal nuclei as in the *Cypripedium* spp. investigated by her in 1908 (see Maheshwari, 1937, p. 374).

## V. Conclusion and Summary

The Adoxa type of embryo sac, formerly called "Lilium type" is characterized by the occurrence of a single nuclear division following the formation of the megaspore nuclei; the mature embryo sac is eight-nucleate and is organized into a normal egg apparatus of three cells and a group of three antipodal cells, leaving two free nuclei which function as polars. The name "Lilium type" is no longer applicable to this mode of development, as *Lilium* conforms to the Fritillaria type where we have a fusion of three of the megaspore nuclei and the interpolation of a secondary four-nucleate stage.

Up to the present, the Adoxa type is known with certainty in relatively few species: *Adoxa moschatellina*, *Smabucus racemosa*, *S. canadensis*, *S. ebulus*, *Erythronium albidum* and *Tulipa ostroviskiana*. In *T. sylvestris* and *T. tetraphylla*, which may provisionally be included here, the development follows a somewhat peculiar course: The megaspore nuclei take up a 3+1 position, so that after the next division six nuclei are seen at the micropylar end and two at the chalazal. In *T. sylvestris* the egg apparatus consists of six cells leaving two free nuclei to function as polars; in *T. tetraphylla* there are five cells at the micropylar end and one at the chalazal, and two free nuclei.

In a few genera, viz., *Ulmus*, *Tamarix*, *Rudbeckia*, *Armeria* and some others, the development is ordinarily of the Fritillaria type, but the Adoxa type also occurs in a small percentage of the ovules. In one individual of *Leontodon hispidus*, the development showed a deviation from the usual monosporic type in more than 50% of the ovules. Here the partition walls laid down between the megaspores became mucilaginous and dis-

solved away leaving all four nuclei in a common cavity. Only one further division occurred giving rise to the eight nuclei of the mature embryo sac.

In the past, several genera were reported to have an embryo sac of the Adoxa type. These must now be transferred elsewhere either because a reinvestigation has shown the previous results to be incorrect or because there is strong evidence of an indirect nature to warrant such removals.

Species of *Piper, Heckeria, Myicaria, Armeria, Statice* (except *S. Eu-Limonium* in which Penaea type has been reported), *Fritillaria, Lilium, Gagea, Cardiocrinum* and *Tulipa* (Sect. Leptostemones) have embryo sacs of the Fritillaria type. It is possible that *Medeola* and some species of *Smilacina* may also belong here.

*Helosis, Thea, Alisma, Sagittaria, Limnocharis* and *Convallaria* have been shown to have bisporic embryo sacs of the Allium type and probably the same will also be found to be true of *Phoradendron, Rhopalocnemis, Lemna* and *Crinum*. The last four need further study, however.

Reports of the occurrence of the Adoxa type in the following genera are considered incorrect or extremely doubtful: *Salix, Juglans, Thesium, Hydnora, Balanophora, Mesembryanthemum, Stellaria, Isomeris, Sedum, Philadelphus, Medicago, Lupinus, Melilotus, Cicer, Euphorbia, Carica, Phyllocactus, Eugenia, Trapa, Forsythia, Fouquieria, Solanum, Rhytidophyllum, Acanthus, Myoporum, Typha, Zea, Cocos, Chamaerops, Homalonema, Aglaonema, Acorus, Commelina, Cynastrum, Aloe, Agave, Cooperia, Amaryllis, Buphane, Nerine, Cyrtanthus, Haemanthus, Costus, Epidendrium, Bletia, Epipactis*, and *Gyrostachys*. It seems likely that in all of these the development is really of the monosporic eight-nucleate type. Further confirmatory evidence is desired however in a few cases: *Isomeris, Cicer, Cocos, Homalonema* and *Aglaonema*.

The embryo sac of *Limnanthes douglasii*, according to the latest account of Fagerlind (1939), shows an extraordinary variability in its development and does not seem to agree with any of the well-known types of development. Four nuclear divisions intervene between the megaspore mother cell and the formation of the egg apparatus and the number of nuclei in the mature embryo sac varies from nine to five, owing to the failure of some divisions at the chalazal end.

In *Pyrethrum balsaminatum* also, the embryo sac is not of the Adoxa type as once reported by Ward. Fagerlind has shown that after the meiotic divisions are over, the three chalazal megaspore nuclei do not take any further part in the development and it is the micropylar nucleus alone which undergoes three divisions to give rise to the eight nuclei of the mature stage. It is a matter of opinion whether such an embryo sac should be regarded as tetrasporic or monosporic. Since the degenerating megaspore nuclei are not cut off from the embryo sac by a wall, Fagerlind is of the opinion that it should be included under the tetrasporic types.

## VI. Acknowledgments

The writing of this paper was begun several years ago in India, continued at Harvard University, Cambridge, Massachusetts, and completed at the University of Notre Dame, Notre Dame, Indiana. I have pleasure in offering my sincere thanks to Profs. R. H. Wetmore and Theodor Just for the assistance which they rendered in its preparation. I am indebted to Miss Joann Walsh, Notre Dame, for the willingness and care with which she typed the manuscript.

## VII. LITERATURE CITED

Agharkar, S. P. and Banerji, I. 1930. The development of the embryo sac in *Carica papaya*. Jour. Dept. Sci. Calcutta Univ. **10**: pp. 10.

Andersson, A. 1931. Studien über die Embryologie der Familien Celastraceae, Oleaceae und Apocynaceae. Acta Univ. Lund Avd. 2, **27**: pp. 112.

Bambacioni, V. 1928a. Ricerche sulla ecologia e sulla embriologia di *Fritillaria persica* L. Ann. di Bot. (Roma) **18**: 7–37.

———. 1928b. Contributo alla embriologia di *Lilium candidum* L. R. C. Accad. Lincei **8**: 612–618.

——— and Giombini, A. 1930. Sullo sviluppo del gametofito femminile in *Tulipa gesneriana* L. Ann. di Bot. (Roma) **18**: 373–386.

Bambacioni-Mezzetti, V. 1931. Nuove ricerche sull-embriologia delle Gigliaceae. Ann. di Bot. (Roma) **19**: 365–382.

Banerji, I. and Venkateswarlu, V. 1936. A preliminary note on the development of the female gametophyte in *Costus speciosus* L. Curr. Sci. **4**: 414.

Battaglia, E. 1941. Contributo all'embriologia delle Tamaricaceae. Nuovo Giorn. Bot. Ital. N.S. **48**: 575–612.

———. 1942. Alcune osservazioni sullo sviluppo del gametofito femmineo della *Myricaria germanica* Desv. Nuovo Giorn. Bot. Ital. N.S. **49**: 464–466.

Bauch, K. 1911. Beiträge zur Entwicklungsgeschichte und physiologischen Anatomie der Palmenblüte. Diss. Berlin.

Bergman, B. 1935. Zytologischen Studien über die Fortpflanzung bei den Gattungen *Leontodon* und *Picris*. Svensk bot. Tidskr. **29**: 155–301.

Bhaduri, P. N. 1932. The development of the ovule and embryo sac in *Solanum melongena*. Jour. Indian Bot. Soc. **11**: 202–224.

Billings, F. H. 1901. Beiträge zur Kenntnis der Samenentwickling. Flora **88**: 253–318.

———. 1933. Development of the embryo sac in *Phorandendron*. Ann. Bot. **47**: 261–278.

———. 1937. Some new features in the reproductive cytology of Angiosperms, illustrated by *Isomeris arborea*. New Phytol. **36**: 301–326.

Brown, W. H. and Sharp, L. W. 1911. The embryo sac of *Epipactis*. Bot. Gaz. **52**: 439–452.

Buell, M. F. 1938. Embryogeny of *Acorus calamus*. Bot. Gaz. **99**: 556–568.

Caldwell, O. W. 1899. On the life history of *Lemna minor*. Bot. Gaz. **27**: 37–66.

Campbell, D. H. 1905. Studies on the Araceae. III. Ann. Bot. **19**: 329–349.

———. 1912. The embryo sac of *Aglaonema*. Scot. Bot. Rev. **1**: 100–115.

Cavara, F. 1899. Studi sul The. Atti. ist. bot. Univ. Pavia 2. Ser. **5**: 265–326.

Chamberlain, C. J. 1897. Contribution to the life history of *Salix*. Bot. Gaz. **23**: 147–179.

Church, M. B. 1916. The development of the embryo sac and embryo of *Cooperia drummondii*. Bull. Torrey Bot. Cl. **43**: 397–405.

Cohen-Stuart, C. P. 1916. Sur le devellopement des cellules generatrices de *Camellia theifera* (Griff.) Dyer. Ann. jard. bot. Buitenzorg **30**: 1–22.

Conard, A. H. 1900. A contribution to the life history of *Quercus*. Bot. Gaz. **29**: 408–418.

Cook, M. T. 1907. The embryology of *Rhitidophyllum*. Bull. Torrey Bot. Cl. **43**: 397–405.

Cooper, D. C. 1933. Macrosporogenesis and embryology of *Melilotus*. Bot. Gaz. **95**: 143–155.

———. 1935. Macrosporogenesis and development of the embryo sac of *Lilium Henryi*. Bot. Gaz. **97**: 346–355.

———. 1936. Macrosporogenesis and embryology of *Medicago*. Jour. Agri. Res. **51**: 471–477.

———. 1937. Macrosporogenesis and embryo sac development in *Euchlaena mexicana* and *Zea mays*. Jour. Agri. Res. **55**: 539–551.

———. 1939. Development of megagametophyte in *Erythronium albidum*. Bot. Gaz. **100**: 362–867.

DAHLGREN, K. V. O. 1916. Zytologische und embryologische Studien über die Reihen Primulales und Plumbaginales. K. Svenska Vetensk.—Akad. Handl. **56**(4): pp. 80.

———. 1918. Die jüngeren Entwicklungsstadien der Samenanlagen von *Typha latifolia* L. Svensk bot. Tidskr. **12**: 207–211.

———. 1928. Die Embryologie einiger Alismataceae. Svensk bot. Tidskr. **22**: 1–17.

———. 1934. Die Embryosackentwicklung von *Echinodorus macrophyllus* und *Sagittaria sagittifolia*. Planta **21**: 602–612.

D'AMATO, F. 1940. Embriologia di *Ulmus campestris* L. Nuovo Giorn. Bot. Ital. N.S. **47**: 247–263.

———. 1940a. Contributo all'embriologia delle Plumbaginaceae. Nuovo Giorn. Bot. Ital. N.S. **47**: 349–382.

DASTUR, R. H. 1922. Notes on the development of the ovule, embryo sac and embryo of *Hydnora africana* Thumb. Trans. Roy. Soc. S. Africa **10**: 27–31.

DAVID, E. 1938. Embryologische Untersuchungen an Myoporaceen, Salvadoraceen, Sapindaceen und Hippocrateaceen. Planta **28**: 680–703.

D'HUBERT, E. 1896. Recherches sur le sac embryonnaire des plantes grasses. Ann. Sci. nat. Bot. Sér. 8, **2**: 37–128.

EKAMBARAM, T. AND PANJE, R. R. 1935. Contribution to our knowledge of *Balanophora*. II. Life history of *B. dioica*. Proc. Indian Acad. Sci. B. **1**: 522–543.

EKDAHL, I. 1941. Die Entwicklung von Embryosack und Embryo bei *Ulmus glabra* Huds. Svensk bot. Tidskr. **35**: 143–156.

ELST, P. VAN DER. 1909. Bijdrage tot de Kennis van de Zaadknopontwikkeling der Saxifragaceen. Diss. Utrecht.

ENGLER, A. 1936. Syllabus der Pflanzenfamilien. 11th ed., Berlin. (Revised by L. Diels).

ERNST, A. 1901. Beiträge zur Kenntnis der Entwicklung des Embryosackes und des Embryos von *Tulips gesneriana* L. Flora **88**: 37–77.

———. 1914. Embryobildung bei *Balanophora*. Flora **106**: 129–159.

EYSEL, G. 1937. Die Embryosackentwicklung von *Limnanthes douglasii* R. Br. Diss. Marburg, pp. 29.

FAGERLIND, F. 1938. Wo kommen tetraporische durch drei Teilungsschritte vollentwickelte Embryosäcke unter den Angiospermen vor? Bot. Notiser **1938**: 461–498.

———. 1938a. Bau und Entwicklung der floralen Organe von *Helosis cayennensis*. Svensk bot. Tidskr. **32**: 139–159.

———. 1939. Kritische und revidierende Untersuchungen über das Vorkommen des Adoxa ("Lilium")—Typs. Acta Horti Bergiani **13** (1): pp. 49.

———. 1939a. Drei Beispiele des Fritillaria-Typus. Svensk bot. Tidskr. **33**: 188–204.

———. 1941. Die Embryosackentwicklung bei *Camassia*. Svensk bot. Tidskr. **35**: 258–260.

———. 1944. Der tetrasporische Angiospermen-Embryosack und dessen Bedeutung für das Verhältnis der Entwicklungsmechanik und Phylogenie des Embryosacks. Ark. f. Bot. **31A** (4): pp. 71.

———. 1945. Bildung und Entwicklung des Embryosacks bei sexuellen und agamospermischen *Balanophora*-Arten. Svensk bot. Tidskr. **39**: 65–82.

FARLEY, H. M. AND HUTCHINSON, H. 1941. Seed development in *Medicago* hybrids. I. The normal ovule. Canadian Jour. Res. **19**: 421–437.

FARREL, M. E. 1914. The ovary and embryo of *Cyrtanthus sanguineus*. Bot. Gaz. **57**: 428–436.

FISCHER, A. 1880. Zur Kenntnis der Embryosackentwicklung einiger Angiospermen. Jena. Z. Naturw. N. F. **7**: 9–132.

FOSTER, L. T. 1943. Morphological and cytological studies on *Carica papaya*. Bot. Gaz. **105**: 116–126.

FRIES, TH. C. E. 1919. Der Samenbau bei *Cynastrum* Oliv. Svensk bot. Tidskr. **13**: 295–304.

FRISENDAHL, A. 1912. Cytologische und entwicklungsgeschichtliche Studien an *Myricaria germanica* Desv. K. Svenska Vetensk.-Akad. Handl. **48** (7): pp. 62.

GÄUMANN, E. 1919. Studien über die Entwicklungsgeschichte einiger Saxifragales. Rec. trav. bot. Néerl. **16**: 285–322.

GIBBS, L. S. 1907. Notes on the development and structure of the seed in Alisnoideae. Ann. Bot. **21**: 25–55.
GIBELLI, G. AND FERRERO, F. 1891. Intorno allo sviluppo dell'ovulo del seme della *Trapa natans* L. Malpighia **5**: 156–218.
GIGANTE, R. 1929. Embriologia dell'*Acanthus mollis*. Nuovo Giorn. Bot. Ital. N.S. **36**: 1–33.
GIOELLI, F. 1930. Il gametofito femmineo e l'evoluzione dell'ovulo in seme in *Chamaerops humilis* L. Lav. Ist. bot. Palermo **1**: pp. 24.
———. 1930. Ricerche sullo sviluppo del gametofito femmineo e del polline nel genere *Aloe*. Lav. Ist. bot. Palermo **1**: pp. 24.
GOW, J. E. 1908. Studies in the Araceae. Bot. Gaz. **46**: 35–42.
———. 1913. Observations on the morphology of the Aroids. Bot. Gaz. **56**: 127–142.
GUIGNARD, L. 1881. Recherches d'embryologénie végétale comparée. I. Legumineuses. Ann. Sci. nat. Bot. Sér. 6, **12**: 5–166.
———. 1882. Recherches sur le sac embryonnaire des phanérogames angiospermes. Ann. Sci. Nat. Bot. Sér. 6, **13**: 136–199.
———. 1885. Observations sur les Santalacées. Ann. Sci. nat. Bot. Sér. 6, **20**: 310–372.
———. 1900. L'appareil sexuel et la double fécondation dans les Tulipes. Ann. Sci. Nat. Bot. Sér. 8, **11**: 365–387.
GUPTA, B. L. 1935. Studies in the development of the pollen grain and embryo sac of *Wolffia arrhiza*. Curr. Sci. **4**: 104–105.
HÅKANSSON, A. 1923. Studien über die Entwicklungsgeschichte der Umbelliferen. Acta Univ. Lund, N. F. Avd. 2, **18** (7): pp. 120.
———. 1929. Die Chromosomen in der Kreuzung *Salix viminalis* × *S. caprea* von Heribert Nilson. Hereditas **12**: 1–52.
HALL, J. G. 1902. An embryological study of *Limnocharis emarginata*. Bot. Gaz. **33**: 214–218.
HEILBORN, O. 1921. Taxonomical and cytological studies on cultivated Ecuadorian species of *Carica*. Ark. f. Bot. **17** (12): 1–16.
———. 1928. Taxonomical and embryological notes on *Carica*. Acta Horti Bergiani **9**: 105–108.
HOFMEISTER, W. 1858. Neuere Beobachtungen über Embryobildung der Phanerogamen. Jahrb. wiss. Bot. **1**: 82–190.
HRUBÝ, CH. 1934. A contribution to the cytology and embryology of *Erythronium dens canis* L. Bull. Int. Acad. Sci. Bohême, pp. 1–9.
———. 1938. Embryo sac development in *Erythronium dens canis*. Chron. Bot. **4**: 20–21.
HUMPHREY, J. E. 1896. The development of the seed in Scitamineae. Ann. Bot. **10**: 1–40.
ISHIKAWA, M. 1918. Studies on the embryo sac and fertilization in *Oenothera*. Ann. Bot. **32**: 279–317.
JOHANSEN, D. A. 1936. Morphology and embryology of *Fouquieria*. Amer. Journ. Bot. **23**: 95–99.
JOHNSON, D. S. 1902. On the development of certain Piperaceae. Bot. Gaz. **34**: 321–340.
———. 1910. Studies in the development of Piperaceae I. The suppression and extension of sporogenous tissue in the flower of *Piper betel* L. var. *monoicum* C. Dc. Jour. Expt. Zool. **9**: 715–749.
JOHRI, B. M. 1935. Studies in the family Alismaceae. II. *Sagittaria sagittifolia* L. Proc. Indian Acad. Sci. B. **1**: 340–348.
———. 1935a. Studies in the family Alismaceae. III. *Sagittaria guayanensis* H. B. K. and *S. latifolia* Willd. Proc. Indian Acad. Sci. B. **2**: 33–48.
———. 1936. Studies in the family Alismaceae. IV. *Alisma plantago* L.; *Alisma plantago-aquatica* L.; and *Sagittaria graminea* Mich. Proc. Indian Acad. Sci. B. **4**: 128–138.
———. 1938. The embryo sac of *Limnocharis emarginata* L. New Phytol. **37**: 279–285.
JÖNSSON, B. 1879/80. Om embryosäckens utveckling hos Angiospermerna. Acta Univ. Lund **16**: 1–86.
JOSHI, A. C. 1937. Megasporogenesis in *Aloe vera* Linn. Jour. Indian Bot. Soc. **16**: 297–300.
———, AND KAJALE, L. B. 1936. A note on the structure and development of the embryo sac, ovule and fruit of *Tamarix dioica* Roxb. Ann. Bot. **50**: 421–426.

JOSHI, P. C. 1936. Contribution to the life history of *Stellaria media* L. Proc. Indian Acad. Sci. B. **3**: 8–22.

JUSSEN, FR. J. 1928. Die Haploidgeneration der Araceen und ihre Verwertung für das System. Englers Bot. Jahrb. **62**: 193–283.

KARSTEN, G. 1902. Über die Entwicklung der weiblichen Blüthen bei einigen Juglandaceen. Flora **90**: 316–333.

KHAN, R. 1943. The ovule and embryo sac of *Fouquieria*. Proc. Nat. Inst. Sci. India **9**: 253–256.

KRATZER, J. 1918. Die verwandtschaftlichen Beziehungen der Cucurbitaceen auf Grund ihrer Samenentwicklung. Flora **110**: 275–343.

KRÜGER, M. 1932. Vergleichend-entwicklungsgeschichte Untersuchungen an den Fruchtknoten und Früchten zweier *Solanum*-Chimären und ihrer Elternarten. Planta **17**: 372–436.

KUWADA, Y. 1928. On occurrence of restitution nuclei in the formation of the embryosac in *Balanophora japonica* Mak. Bot. Mag. Tokyo **42**: 117–129.

LAGERBERG, T. 1909. Studien über die Entwicklungsgeschichte und systematische Stellung von *Adoxa moschatellina* L. K. Svenska Vetensk.-Akad. Handl. **44** (4): 1–86.

LAMM, R. 1937. A contribution to the embryology of the potato. Svensk. bot. Tidskr. **31**: 217–220.

LANGDON, LADEMA M. 1934. Embryogeny of *Carya* and *Juglans*, a comparative study. Bot. Gaz. **96**: 93–117.

LEFFINGWELL, A. M. 1903. Morphological study of bulb and flowers of *Camassia quamash* (Purch.) Greene. Res. Stud. St. Coll. Washington **2**: 80–89.

LELIVELD, J. A. 1935. Cytological studies in the genus *Ulmus*. II. The embryo sac and seed development in the common Dutch elm. Rec. Trav. Bot. Néerland. **32**: 543–573.

LOTSY, P. 1899. *Balanophora globosa* Jungh. Eine wenigstens örtlich verwitwete Pflanze. Ann. jard. bot. Buitenzorg **16**: 174–186.

———. 1901. *Rhopalocnemis phalloides* Jungh. A morphological-systematical study. Ann. jard. bot. Buitenzorg, 2 ser. **2**: 73–101.

MAHESHWARI, P. 1937. A critical review of the types of embryo sacs in Angiosperms. New Phytol. **36**: 359–417.

———. 1941. Recent work on the types of embryo sacs in Angiosperms. Jour. Indian Bot. Soc. **20**: 229–261.

———. 1942. The embryo sac of *Euphorbia heterophylla* L. Proc. Indian Acad. Sci. B **15**: 158–166.

———. 1946. The Fritillaria type of embryo sac: a critical review. (In press).

———. AND SINGH, B. 1934. A preliminary note on the morphology of the aerial and underground flowers of *Commelina benghalensis* Linn. Curr. Sci. **3**: 158–160.

MARKOVA, L. G. 1944. Contribution to the embryology of certain representatives of Leguminosae. Jour. Bot. URSS **29** (5): 219–231.

MAURITZON, J. 1933. Studien über die Embryologie der Familien Crassulaceae und Saxifragaceae. Akad. Abh. Lund: pp. 152.

———. 1934. Ein Beitrag zur Embryologie der Phytolaccaceen und Cactaceen. Bot. Notiser **1934**: 111–135.

———. 1935. Über die Embryologie der Familie der Rutaceae. Svensk bot. Tidskr. **29**: 319–347.

———. 1936. Samenbau und Embryologie einiger Scitamineen. Acta Univ. Lund **31**: 1–31.

———. 1936a. Zur Embryologie einiger Parietales-Familien. Svensk bot. Tidskr. **30**: 79–113.

MCALLISTER, F. 1909. The development of the embryo sac of *Smilacina stellata*. Bot. Gaz. **48**: 200–215.

———. 1914. The development of the embryo sac in the Convallariaceae Bot. Gaz. **58**: 137–153.

MCCOLLUM, R. L. 1939. The development of the embryo sac and seed of *Commelina angustifolia* Michx. Bull. Torrey Bot. Cl. **66**: 539–548.

MICHELL, M. R. 1916. The embryo sac of *Richardia africana* Kth. Bot. Gaz. **61**: 325–336.

MILLER, E. C. 1919. Development of the pistillate spikelet and fertilization in *Zea mays* L. Jour. Agri. Res. **18**: 255–266.

MODILEWSKI, J. 1910. Weitere Beiträge zur Embryobildung einiger Euphorbiaceen. Ber. deutsch. bot. Ges. **28**: 414–418.

———. 1928. Die embryologische Entwicklung von *Thesium intermedium* L. Bull. jard. bot. Kieff **7/8**: 65–70.

MÜCKE, M. 1908. Über den Bau und die Entwicklung der Früchte und über die Herkunft von *Acorus calamus*. Bot. Ztg. **66**: 1–23.

NANETTI, A. 1912. Sulla probabili cause della partenocarpia del *Solanum muricatum* Ait. Nuovo Giorn. Bot. Ital. N. S. **19**: 91–111.

NAST, C. G. 1935. Morphological development of the fruit of *Juglans regia*. Hilgardia **9**: 345–381.

NAWASCHIN, S. AND FINN, W. W. 1913. Zur Entwicklungsgeschichte der Chalazogamen, *Juglans regia* und *J. nigra*. Mém. Acad. Sci. St. Pétersb. **31** (8): 1–59.

NEUMANN, M. 1935. Die Entwicklung des Pollens, der Samenanlage und des Embryosackes von *Pereskia amapola* var. *argentina*. Öster. bot. Zeitschr. **84**: 1–30.

NEWTON, W. C. F. 1927. Chromosome studies in *Tulipa* and some related genera. Jour. Linn. Soc. Bot. **47**: 339–354.

NIETSCH, H. 1941. Zur systematischen Stellung von *Cynastrum*. Öster. bot. Zeitschr. **90**: 31–52.

NITZSCHKE, J. 1914. Beiträge zur Phylogenie der Monokotylen, gegründet auf der Embryosackentwicklung apokarper Nymphaeaceen und Helobien. Cohns Beitr. Biol. Pfl. **12**: 223–267.

PACE, L. 1914. Two species of *Gyrostachys*. Baylor Univ. Bull. **17** (1): 1–16.

PALM, B. 1915. Studien über Konstruktionstypen und Entwicklungswege des Embryosackes der Angiospermen. Diss. Stockholm.

PÀROLI, V. 1940. Contributo allo studio embriologico delle Tamaricaceae. Ann. di Bot. (Roma) **22**: 1–18.

PIJL, L. VAN DER. 1934. Über die Polyembryonie bei *Eugenia*. Rec. Trav. bot. Néerland **31**: 113–187.

PURI, V. 1939. Studies in the order Parietales I. A. contribution to the morphology of *Tamarix chinensis* Lour. Beih. bot. Centralbl. **59A**: 335–349.

QUISUMBING, E. AND JULIANO, J. B. 1927. Development of the ovule and embryo sac of *Cocos nucifera*. Bot. Gaz. **84**: 274–293.

RAO, L. N. 1942. Studies in the Santalaceae. Ann. Bot. N. S. **6**: 151–175.

REES-LEONARD, O. L. 1935. Macrosporogenesis and development of the macrogametophyte of *Solanum tuberosum*. Bot. Gaz. **96**: 734–750.

REEVES, R. G. 1930. Development of the ovule and embryo sac of alfalfa (*Medicago sativa* L.) Amer. Jour. Bot. **17**: 239–246.

ROCEN, TH. 1927. Zur Embryologie der Centrospermen. Diss. Uppsala.

ROMANOV, I. D. 1936. Die Embryosackentwicklung in der Gattung *Gagea* Salisb. Planta **25**: 438–459.

———. 1939a. Eine neue Form des Embryosackes von *Adoxa*-Typus bei *Tulipa tetraphylla* und *T. ostroviskiana*. Compt. Rend. (Doklady) Acad. Sci. URSS **19**: 113–115.

———. 1939b. Two new forms of embryo sac in the genus *Tulipa*. Compt. Rend. (Doklady) Acad. Sci. URSS **22**: 139–141.

ROSÉN, W. 1944. The embryo sac of *Rudbeckia*. Göteborg Bot. Trädgard Meddel. **15**: 267–273.

RUTISHAUSER, A. 1935. Entwicklungsgeschichtliche und zytologische Untersuchungen an *Korthalsella Dacrydii* (Ridl.) Danser. Ber. Schweiz. bot. Ges. **44**: 389–436.

———. 1937. Entwicklungsgeschichtliche Untersuchungen an *Thesium rostratum* M. U. K. Mitteil. Naturf. Ges. Schaffhausen **13**: 25–47.

SANCHEZ, S. T. 1938. Embryo-sac development in *Euphorbia heterophylla* Linn. Univ. Philippines Nat. & Appl. Sci. Bull. **6**: 59–75.

SCHAEPPI, H. 1942. Morphologische und entwicklungsgeschichtliche Untersuchungen an den Blüten von *Thesium*. Mitt. Naturw. Ges. Winterthur **23**.

———. AND STEINDL, F. 1937. Blütenmorphologische und embryologische Untersuchungen an *Osyris alba* L. Ber. Schweiz. bot. Ges. **47**: 369–392.
SCHAFFNER, J. H. 1896. The embryo sac of *Alisma plantago*. Bot. Gaz. **21**: 123–132.
———. 1897. The life history of *Sagittaria variabilis*. Bot. Gaz. **23**: 252–273.
———. 1897a. The development of the stamens and carpels of *Typha latifolia*. Bot. Gaz. **24**: 93–102.
———. 1901. A contribution to the life history and cytology of *Erythronium*. Bot. Gaz. **31**: 369–387.
SCHLIMBACH, H. 1924. Beiträge zur Kenntnis der Samenanlagen und Samen der Amaryllidaceen mit Berücksichtigung des Wassergehaltes der Samen. Flora, **117**: 41–54.
SCHMID, W. 1925. Morphologische, anatomische und entwicklungsgeschichtliche Untersuchungen an *Mesembryanthemum pseudotruncatellum* Berger. Beibl. Vierteljahrschr. Naturf. Ges. Zürich **70**: 1–96.
SCHNARF, K. 1929. Embryologie der Angiospermen. Bornträger, Berlin.
———. 1931. Vergleichende Embryologie der Angiospermen. Bornträger, Berlin.
———. 1936. Contemporary understanding of embryo sac development among angiosperms. Bot. Rev. **2**: 565–585.
———. AND WUNDERLICH, R. 1939. Zur vergleichenden Embryologie der Liliaceae, Asphodeloideae. Flora, N. F. **33**: 297–327.
SCHNIEWIND-THIES, J. 1901. Die Reduktion der Chromosomenzahl und die folgenden Kernteilungen in den Embryosackmutterzellen der Angiospermen. Gustav Fischer, Jena.
SCHULLE, H. 1933. Zur Entwicklungsgeschichte von *Thesium montanum* Ehrh. Flora, N. F. **27**: 140–184.
SHARMA, Y. M. L. 1939. Gametogenesis and embryogeny in *Tamarix ericoides* Rottl. Ann. Bot. N. S. **3**: 861–870.
SHARP, L. W. 1912. The orchid embryo sac. Bot. Gaz. **54**: 373–385.
SHATTUCK, C. H. 1905. A morphological study of *Ulmus americana*. Bot. Gaz. **40**: 209–223.
SHUHART, D. V. 1932. Morphology and anatomy of the fruit of *Hicoria pecan*. Bot. Gaz. **93**: 1–20.
SIMONI, D. 1937. Osservazioni sulla fertilita e ricerche citologiche-embryologiche in *Tulipa Gesneriana* L. Boll. Soc. Ticinese di Sci. Nat. **32**.
SMITH, F. H. 1942. Development of the gametophytes and fertilization in *Camassia*. Amer. Jour. Bot. **29**: 657–663.
STENAR, H. 1925. Embryologische Studien. I. Zur. Embryologie der Columniferen. II. Die Embryologie der Amaryllideen. Akad. Abh. Uppsala.
———. 1925a. Embryologische und zytologische Studien über *Limnanthes Douglasii* R. Br. Svensk bot. Tidskr. **19**: 133–152.
———. 1927. Über die Entwicklung des siebenkernigen Embryosackes bei *Gagea lutea* Ker. Svensk bot. Tidskr. **21**: 344–360.
———. 1934. Embryologische und zytologische Beobachtungen über *Majanthemum bifolium* und *Smilacina stellata*. Ark. f. Bot. **26**: 1–20.
———. 1937. Vorläufige Mitteilung über die Embryologie einiger Liliifloren. Naturvetenskapl. För. :s i Östersund förhandl. Jämten. Uppsala. Pp. 245–246.
———. 1941. Ueber die Entwicklung des Embryosackes bei *Convallaria majalis* L. Bot. Notiser **1941**: 123–128.
STIFFLER, E. G. 1925. Development of embryo sac in *Gasteria, Cyrtanthus* and *Veltheimia*. Bot. Gaz. **79**: 207–216.
TISCHLER, G. 1942/43. Allgemeine Pflanzenkaryologie, **2**: Bornträger, Berlin.
TOMITA, K. 1931. Über die Entwicklung des nackten Embryos von *Crinum latifolium*. L. Sci. Rep. Tôhoku Univ. **6**: 163–169.
TREUB, M. 1898. L'organe femelle et l'apogamie du *Balanophora elongata*. Ann. jard. bot. Buitenzorg **15**: 1–25.
———. AND MELLINK, J. 1880. Notice sur le développement du sac embryonnaire dans quelques Angiospermes. Arch. Néerland. Sci. **15**: 452–457.
UMIKER, O. 1920. Entwicklungsgeschichtlich-zytologische Untersuchungen an *Helosis guayensis* Rich. Diss. Zürich.
USTERI, A. 1907. Studien über *Carica papaya* L. Ber. deutsch. bot. Ges. **25**: 485–495.

VAN TIEGHEM, PH. 1896. Sur l'organisation florale des Balanophoracées et sur la place cette famille dans le souclasse des Dicotylédones inovulées. Bull. Soc. Bot. France **43**: 295–310.

———. 1907. Sur les Inovulées. Ann. Sci. Nat. Bot. Sér. 9, **6**: 125–260.

WALKER, R. I. 1938. Macrosporogenesis and embryo development in *Ulmus fulva*. Bot. Gaz. **99**: 592–598.

WARD, H. M. 1880. A contribution to our knowledge of the embryo sac in Angiosperms. Jour. Linn. Soc. London Bot. **17**: 519–546.

WEATHERWAX, P. 1919. Gametogenesis and fecundation in *Zea mays* as the basis of xenia and heredity in the endosperm. Bull. Torrey Bot. Cl. **46**: 72–90.

WIEGAND, K. M. 1900. The development of the embryo sac in some monocotyledonous plants. Bot. Gaz. **30**: 25–47.

WOODROOF, N. C. 1928. Development of the embryo sac and young embryo of *Hicoria pecan*. Amer. Jour. Bot. **15**: 416–421.

WOYCICKI, Z. 1929. Die Entwicklung des Embryosackes bei *Haemanthus katharinae*. Acta Soc. Bot. Polon. **6**: 193–202.

YOUNG, W. J. 1905. The embryology of *Melilotus alba*. Proc. Indiana Acad. Sci., **1905**: 133–141.

———. 1923. The formation and degeneration of germ cells in the potato. Amer. Jour. Bot. **10**: 325–335.

ZABBAN, B. 1936. Osservazioni sulla embriologia di *Myricaria germanica* Desv. Ann. di Bot. (Roma) **21**: 301–321.

ZWEIFEL, R. 1939. Cytologisch-embryologische Untersuchungen an *Balanophora abbreviata* Blume und *B. indica* Wall. Diss. Zürich.

# Type Studies on Agarics-II[1]

ROLF SINGER

(*Farlow Herbarium, Harvard University, Cambridge, Mass.*)

This is a continuation of the studies on type and authentic specimens preserved in the herbaria of this country. While most of the types examined in part I came from the Herbarium of the New York Botanical Garden, the present part deals with specimens preserved at the Farlow Herbarium (Curtis Herbarium, Patouillard Herbarium, Höhnel Herbarium, etc.) and at the Herbarium of the Agricultural Experiment Station of the University of Florida (FLAS.)

## Fam. TRICHOLOMATACEAE

TRICHOLOMA LACTESCENS Pat., Bull. Soc. Myc. Fr. **23**: 59. 1917. (Type, and color-plates.)

The type has a pinkish spore print like that of *Collybia butyracea;* the spores are smooth to distinctly though very minutely rough, thin-walled, without suprahilar depression, non-amyloid, hyaline, 5–5.5×3.2–4μ; basidia and cystidia none seen, the hymenium of the type being partly destroyed; laticiferous hyphae present but not predominant; gill trama regular, consisting of rather parallel, hyaline hyphae which have rather thin, non-amyloid walls, a diameter of 3–10μ, and clamped septa.

This species is illustrated by two excellent plates in V. Demange's unpublished Album in the Farlow Library. It has all the characters of a *Rhodopaxillus*, and therefore the name **Rhodopaxillus lactescens** (Pat.) Sing. comb. nov. is proposed.

AERUGINOSPORA SINGULARIS Hoehn., Sitz.-ber. k. Akad. Wiss. Wien **117**: 1012, 1908. (Type.)

The spores of this species are non-amyloid, thin-walled, pore-less; the hyphae are non-amyloid, the septa clampless; the basidia are medium sized, 27×6.5μ, and 4-spored. The external appearance of the dried carpophores is that of a *Clitocybe*. There is no spore print preserved, together with the specimens, and the lamellae are now grayish.

These additional characters prove that *Aeruginospora* has neither any relationship to the other green-spored agarics (provided it is, itself, really green spored which has been doubted), nor is it congeneric with *Clitocybe*. I am inclined to think that *Aeruginospora singularis* is a tropical species of *Armillariella*, in which case the short spores, clampless septa, decurrent lamellae, and slightly colored spore print would fit into the generic diagnosis.

[1] Cf. Singer, Rolf. Type Studies on Agarics. Lloydia **5**: 97–135. 1942.

AGARICUS (COLLYBIA) BORYANUS Berk. & Mont., Ann. Sc. Nat. III. 11: 235. 1849. (Authentic[2].)

These specimens darken much more in the herbarium than do those of *Lentinus cubensis* and—although the microscopical characters are not easily ascertained in the specimens available—the general appearance, shape, and color of the carpophores is too different to allow one to synonymize these species. The writer has found a species very similar to the Cuban specimens of *Agaricus Boryanus* which will be described in a later paper. However, I want to emphasize that they are not identical with what Murrill has called *Armillaria Boryana* (Berk. & Mont.) Murr. The latter is, as I have been able to find out by comparison and by observation of living plants, the same as *Lentinus cubensis* Berk. & Curt. (see Lloydia **5**: 130. 1942): about this latter species, see p. 124 of the present paper.

AGARICUS (MYCENA) IOCEPHALUS Berk. & Curt., Ann. Mag. Nat. Hist. II. **12**: 420. 1853. (Type and fresh material compared with the type.)

*Pileus* "Aconite violet" to "light Perilla purple," margin becoming "light purplish lilac" or even paler, center sometimes becoming as deeply colored as "dark Perilla purple," somewhat hygrophanous, paler when dry, radially striate to sulcate, convex, later flattened or irregular, rather thin, glabrous, non-viscid, 12–45 mm. broad.—*Lamellae* between "pale vinaceous lilac" and "light vinaceous lilac," subdistant to distant, narrow, 1–2 mm. broad, free to adnexed; spore print almost pure white, much paler than in *C. butyracea*.—*Stipe* white when quite young, soon becoming "pale vinaceous lilac" to "light purple drab" above, the base "tilleuil buff" or sordid, the very base reaching "clay color" and coarsely strigose-tomentose, often the entire stipe pilose with white hairs, more often glabrous at the apex, tapering upwards, 35–60×1.5–5 mm.—*Context* subconcolorus-paler; odor of sauerkraut (disagreeable); taste not distinctive.

*Spores* 7.5–8×3.5–4μ, elongate-ellipsoid, with the whole inner side more or less applanate, smooth, non-amyloid, hyaline; *basidia* 4-spored; *cystidia* none; *cheilocystidia*-like bodies on the partly sterile edge not forming a continuous hymenium; *hyphae of the cuticle* filamentous, lilac with dissolved pigment turning blue in alkali, repent; all hyphae non-amyloid, with clamp connections.

The color of the pigment as found in nature is due to a slightly acid reaction of the cell sap; it becomes "roselline purple" with strong acids ($HNO_3$), and "Delft blue" with alkali (e.g., $NH_4OH$). This blue reaction is still distinct in dried material.

On fallen leaves characteristic of southern low hammock vegetation, preferring leaves of *Liquidambar styraciflua* but also on leaves of *Quercus nigra*, *Pinus palustris*, *Ostrya virginiana*, *Acer rubrum*, *Nyssa sylvatica*,

[2] Material in the Curtis Herbarium and in Wright's Fungi Cubenses (det. Berkeley).

fruiting in June, July and August. From New York to North Florida and west to Alabama.

The pigment reacts as an indicator in a manner comparable to the reaction of the pigment of *Lactarius turpis*. The anatomical data given above prove that this species has nothing in common with *Mycena*, nor is it a *Marasmius* as Pennington and others thought, but that it belongs to *Collybia*. The combination **Collybia iocephala** (B. & C.) Sing. comb. nov. is proposed.

AGARICUS (COLLYBIA) LUTEOOLIVACEUS Berk. & Curt., Ann. Mag. Nat. Hist. III. 4: 286. (Type, and fresh material compared with the type.)

*Pileus* uniformly yellowish-melleous with sometimes umbrinous hues, hygrophanous, "Isabella color" when wet, "chamois" to "honey color," or "cartridge buff" when dry, occasionally "olive ocher" on the disc, long but faintly transparently striate when wet, smooth when dry, glabrous, becoming copper red ("liver brown," "carob brown" at the darker places, as pale as "walnut brown" on the lighter colored places) where it has dried out completely and in the herbarium, campanulate or more often convex, umbilicate, becoming subumbilicate, when dried with depressed center, with projecting margin, sometimes becoming flattened in age, the cuticle not gelatinized, even when quite wet, 12–26 mm. broad.—*Lamellae* concolorous with the pileus in fresh as well as in dried condition, or "buff yellow," sometimes paler than the pileus in youth, close to crowded, with entire and concolorous edge, or sometimes somewhat eroded, moderately broad, or sometimes narrow, adnate to subdecurrent, or emarginate-adnexed, separating on drying; spore print white when fresh.—*Stipe* concolorous with the pileus or lamellae, excepting the pure white and unchanging mycelial tomentum which is always well developed, somewhat pruinate, then glabrous, smooth, often slightly compressed, opaque, equal or very slightly tapering upwards, fleshy-cartilaginous, solid, or hollow in age, 22–55×1.5–5 mm.—*Context* concolorous with the surface, fleshy-fibrous, soft, later rather somewhat tough, but fragile when fresh, rather thin; odor none; taste disagreeable, styptic, more or less bitter.

*Spores* 4.5–6.2×3.2–4μ, ellipsoid, smooth, thin-walled, non-amyloid, non-pseudoamyloid, without germ pore, hyaline or more rarely with a rosy-vinaceous cell sap, the majority with vinaceous red oil droplet or red pigment precipitation along the inside of the wall or with red intracellular crystals, at least in dried material, and older spore prints; *basidia* 16.5–27×(4)–4.5–6.5μ, with or without deep red guttulae or amorphous or crystalline bodies, at least in herbarium material, 4-spored; *cystidia* and cheilocystidia none; *cystidiols* (or basidiols as for some of them) fusiform or basidiomorphous, or fusoid-lageniform, very sparse to rather numerous along the edges of the gills, always hyaline, also often filamentous-sub-

flexuous, or subcapitate at times, 16–28×1.5–4.8μ; *edge* homomorphous; *trama* regular, consisting of subparallel-subinterwoven to parallel, moderately thick hyphae, sometimes with some of the red pigment found in the spores and basidia, septa moderately distant, without clamps; *cuticle* of repent hyphae; *epicutis* little differentiated. The reddening of the carpophore can also be induced by various reagents. On stumps, logs, and trunks of oak, birch, and pine (e.g. *Pinus glabra*), gregarious, fruiting from June till October. From New England to North Florida and west at least to Tennessee.

This species varies to a certain degree in certain particularities, and this being a rather rare species, its identification with extreme forms is not always easy. Even so, the microscopical characters of the dried plant are so striking that it would not have been difficult to determine our first specimens (*C. psilocybe* Murr. & Sing.) as *Collybia luteoolivacea* (Berk. & Curt.) Sacc. if the latter had been known and described adequately. It was necessary to restudy the types of the Curtis Herbarium in order to establish the identity of both of these species. I think that *Agaricus coloreus* Peck and *A. rubescentifolius* Peck too belong to this species. It is, however, a mistake to identify these fungi with the European *Agaricus exsculptus* Fr. which is evidently nothing but a yellow form of *Collybia dryophila*. *Callistosporium* does not occur in Europe. I propose the new combination **Callistosporium luteoolivaceum** (Berk. & Curt.) Sing.

COLLYBIA IRRORATA Pat., *in* Duss, Enum. Champ. Guadel., p. 49. 1903.

The type and two additional collections, with drawings are preserved in the Patouillard Herbarium (FH). To the characters already indicated by Patouillard, I want to add several more.

Spores ellipsoid, thin-walled, these as well as the hyphae non-amyloid; cystidia very thick-walled, with a hood of calcium oxalate; hyphae partly thick-walled, partly thin-walled, they have few septa and these are very difficult to observe. I think, however, I have seen at least three good clamp connections, and several more septa without clamps, thus, the clamp connections appear to be scattered and not constant in the tissue; the cellular cuticle consists of spherocysts filled with dark brown pigment; the material is outwardly in very good condition but there is *Actinomyces* in most of it. For more details see Patouillard's diagnosis, l.c.

This species seems to be rather closely related to *Pseudohiatula Cyatheae* (Sing.) Sing. (*Mycena Cyatheae* Sing.) which Kühner thought might be included in *Marasmius*. Whether this group of fungi, perhaps including the clampless species *Marasmius esculentus* and *"Collybia" conigenoides*,[3] is

[3] I have studied the type and numerous other collections, and there is no doubt about its position in the immediate neighborhood of *M. esculentus*. The host is a *Magnolia* sp. Clamp connections are absent.

considered as belonging to *Marasmius*, or to a genus by itself, depends entirely on the definition of the genus. In my opinion, *Pseudohiatula*, though undoubtedly related to *Marasmius*, sect. *Alliacei*, is as good a genus as is now generally admitted in botany, and, therefore, the combination **Pseudohiatula irrorata** (Pat. *in* Duss) Sing. comb. nov. is proposed for *Collybia irrorata* Pat.

Murrill synonymizes this species with *Gymnopus nigritus* (Berk. & Curt.) Murr. However, the type of *Agaricus* (*Collybia*) *nigritus* Berk. & Curt. is identical with *Hydropus fuliginarius* (Batsch ex Fr.) Sing. (see below).

OMPHALOPSIS PERNIVEA Murr., Proc. Fla. Acad. Sc. **7**: 113. 1944 (publ. 1945).

The type consists of a scanty collection from sandy soil under a palmetto palm in Gainesville (North Florida). It has dermatocystidia of 15–22×6.7–11.3μ which are numerous on the pileus, clavate balloon-shaped, and on the stipe there are similar, more irregular and narrower bodies; the hyphae of the stipe are strongly parallel; on and very near to the edge of the lamellae, I found cheilocystidia of the same general shape as the dermatocystidia of the pileus; basidia 20–26×6.3–6.7μ, mostly 4-spored; all hyphae were non-amyloid. The spores which were seen by Murrill as well as by me, were narrowly oblong, subcylindric, about 8×3.3μ or still narrower, non-amyloid, smooth.

If these spores belong to the specimen, then, Murrill's plant is different from an otherwise very similar species (described below), and does not even belong in the same genus. However, the near-identity of the anatomical characters and the very suggestive habitat (though on the base of the palms instead of on the trunk) brings up the question whether *Omphalopsis pernivea* is a different species, or a *nomen ambiguum* in which the sterile portions and the basidia belong to the following species (*Hydropus Sabalis*) while the spores are foreign (which often happens when small agarics are left near or under other fungi with which they have been collected or studied). There are other slight differences between the palm *Hydropus* and Murrill's plant in the macroscopical description, but they would hardly be important enough to warrant separation if the matter of the spores had not been discovered. I therefore feel that the common and interesting palm inhabiting fungus of South Florida with short and broad amyloid spores should here be described, for comparison, as a new species of *Hydropus* (Kühn.) Sing.

**Hydropus** (Kühn.) Sing. stat. nov. (*Mycena* sect. *Hydropus* Kühn., Mycen., p. 531, 1938) with the following species: *H. marginellus* (Pers. ex Fr.) Sing.; *H. fuliginarius* (Batsch ex Fr.) Sing. (type of the genus; syn.: *Agaricus nigritus* B. & C.); *H. africanus* Sing.; **H. atriceps** (Murr. as *Gymnopus*) Sing. comb. nov.; **H. translucens** (Murr. as *Camarophyllus*)

Sing. comb. nov.; *H. Sabalis* Sing. spec. nov. (see below), and *H. oculatus* (Murr.) Sing.

**H. Sabalis** Sing. nov. sp. Pileo albo, glabro, striato, umbilicato, 12–25 mm. lato; dermatocystidiis numerosis vesiculosis. Lamellis albis, sublatis, arcuatis, decurrentibus, sat distantibus; sporis albis, s.m. hyalinis, amyloideis, breviter ellipsoideis vel subglobosis, levibus, 6.5–7.5×5.3–6μ; cheilocystidiis 20–66×6.8–17μ; tramate haud amyloideo. Stipite albo, fistuloso, glabro, 15–37×1–3 mm. Carne alba; odore nullo; sapore miti. Hyphis fibuligeris.

*Pileus* white, hygrophanous, non-viscid, glabrous, naked, transparently striate when wet, convex with depressed center or umbilicate, later concave with the margin sometimes strangely uplifted, 12–25 mm. broad.—*Lamellae* white, medium broad, more rarely broad (2–3 mm.), arcuate, eventually strongly descendant, always deeply decurrent, rather distant, entire, intermixed with lamellulae; spore print white.—*Stipe* white, glabrous, naked, smooth, but the base white strigose, fistulose, equal, or thickened upwards or downwards, 15–37×1–3 mm.—*Context* white, thin, fragile and fleshy; odor none; taste mild.

*Spores* 6.5–7.5×5.3–6μ, short ellipsoid to subglobose, smooth, without suprahilar depression, amyloid; *basidia* 20–25.5×6.2–6.8μ, 4-spored; *cheilocystidia* on or near the edge, 20–66×6.8–17μ, vesiculose to clavate-balloon shaped, sometimes minutely mucronate at the apex with a apiculate papilla on the tip, or acuminate at the tip, rarely capitulate, thin-walled, easily collapsing, hyaline; *cystidia* none; *trama* regular but the outermost layer (nearest the hymenium) distinctly though slightly diverging without being otherwise differentiated from the mediostratum, but becoming quite regular in mature specimens, consisting of hyaline, non-amyloid hyphae of variable length and diameter; *hyphae of the pileus* rather irregularly interwoven, more parallel-prostrate in the hypodermium where some occasional laticiferous hyphae are intermixed, rather filiform and thin; *epicutis* consisting of occasionally interrupted fascicles or groups of dermatocystidia, especially near the margin of the pileus where they have the same appearance and shape as the cheilocystidia; the same *dermatocystidia* on the stipe are, however, often more irregular and narrower; hyphae of the interior of the stipe-context strictly parallel; all *septa* with clamp connections.—$FeSO_4$ negative.

This is the most specialized of the smaller, non-symbiotic agarics in Florida. It occurs only on living trunks of *Sabal palmetto*, gregarious, sometimes associated with *Mycena chlorinosma* Sing.[4] which has a preference for palmetto. Fruiting from July till November. South Florida, in the

[4] This was discovered in a greenhouse of the Botanical Garden in Leningrad. It was an exciting experience for this writer to find this species in the hammocks of South Florida from where it must have been introduced to Europe.

tropical and subtropical zones, common in Highlands Hammock State Park and in and around the Fairchild Tropical Garden, rarely found on other palms related to *Sabal palmetto*, in gardens, alleys etc.

This species is most closely related to *H. translucens* (Murr. Mycologia **35**: 424. 1943) Sing. which differs in having still more distant lamellae than our species, smaller [in the type specimen (FLAS) 5.5–6.5×4–4.8] spores, and the habitat on earth under hardwood; the dermato- and cheilocystidia, the iodine reaction, the lack of pigment, and many other features are the same in this as well as in our species.

MARASMIUS SEMIUSTUS Berk. & Curt.. Journ. Linn. Soc., Bot. **10**: 295. 1868. (Type and various additional collections, also fresh, and compared with the type.)

*Pileus* white, subglabrous, radially sulcate and slightly grooved, convex, then flat, more or less umbilicate, 7–22 mm. broad, rarely broader.—*Lamellae* white, medium broad to rather broad (1–2.8 mm.), distant (8–15 through-lamellae), not or slightly ventricose, adnexed to adnate, more rarely somewhat subdecurrent, lamellulae 0—many, in 1–3 tiers, spore print white.—*Stipe* white, subglabrous, curved, rarely straight, attached to a somewhat pruinate pedestal (or insiticious, the lower part frequently becoming brownish in old and long-stemmed forms), tapering upwards or downwards, or equal, eccentric, rarely central, 3–20×0.2–2 mm.—*Context* white, thin, submembranaceous, not fragile. Odor none.

*Spores* (6)–7–10.8×(4)–4.5–6μ, non-amyloid, smooth, hyaline, without suprahilar depression, sometimes even convex on the inner side, ellipsoid to ellipsoid-oblong; *basidia* 21–35×5.5–9.5μ, 4-spored, basidioles fusoid; *cheilocystidia* 21–30×6–10μ, but also smaller or larger than this, very variable in shape and size, clavate with nodulose or capitate subsessile appendages all over, or vesiculose and echinate-appendiculate, sometimes with not more than one oblique appendage, more frequently with innumerable appendages either concentrated near the tip, or equally dense on the sides, the appendages sometimes branched, the whole cheilocystidiam also often branched, and the branches lacerate-digitate, numerous; *edge* of gills heteromorphous; *subhymenium* of thin and short, strongly interwoven hyaline hyphae forming a thick layer; *trama* regular, consisting of interwoven, hyaline, slightly thick-walled, non-amyloid hyphae; *hyphae* of the pileus somewhat thick-walled, irregular, less thick-walled, and less irregular in the hypodermium; the *epicutis* strongly differentiated, consisting of strongly diverticulate hyphae, some of them branched nearly rectangularly, the branches also diverticulate and, if erect, assuming the character of dermatocystidia which are entirely analogous to the cheilocystidia of the lamellae; all *hyphae* with clamp connections and nonamyloid; *surface of the stipe* also more or less diverticulate.

On various Cormophyta, e.g., *Caryota mitis* (Fla.), *Saccharum officinarum* (La.); *Pithecolobium samon* (Cuba), etc. on dead as well as living material, roots, wood, vines, especially bark, often in large quantity climbing up the trunks in the tropical forests, 6–10 ft. from the ground, fruiting from May until September.

Material studied: CUBA (Fungi Cub. Wright and Curtis Herb., FH, type); Soledad, Cienfuegos, *W. L. White, 470* (FH); *D. H. Linder*, on sugar cane (FH).—FLORIDA: Miami, *R. Singer F 1500* on *Caryota* (FH).—LOUISIANA: Lobdell, *H. R. Fulton*, on sugar cane (FH), also St. Delphine, La. (FH).

When growing on sugar cane, it often causes root disease in the Americas (in Asia, the disease seems to be mostly caused by a similar species, known as *Marasmius plicatus* or *M. Sacchari*, and phytopathologists frequently determine the American root disease erroneously under these names). It is "omnivorous" and will probably be found to cause damage also on crops other than sugar cane. Its taxonomic position is, together with a series of other species, ambiguous between *Marasmius*, section *Rameales* Kühner, and *Hemimycena*, sect. *Pseudoconidiophorae* Sing. In fact, these tropical species seem to make impossible the clear separation of *Hemimycena* and *Marasmius* on this level. It would in my opinion be best to remove the whole section *Rameales* from the *Marasmii* and incorporate them in *Hemimycena*.

Murrill identifies *M. semiustus* with *M. stenophyllus* Mont. the type of which I have not studied. However, the description, if it is anywhere near the facts, excludes such a synonymy (lamellae foldlike in Montagne's species). Otherwise, his description (North Am. Flora **9**: 262. 1915) comes rather close to my own in some items. I have seen the specimens on banana trash, mentioned by Murrill but have not studied them. They probably belong here. *M. hyperellus* Fr. cannot be considered as belonging here unless there are specimens that, in spite of the description, prove their identity with *H. semiusta*.

PANUS CANTHARELLOIDES Mont., Ann. Sc. Nat. IV. **1**: 120. 1854. Type.
MARASMIUS PURPURASCENS Berk. & Curt., Journ. Linn. Soc., Bot., **10**: 296. 1868. (Type.)
LENTINUS SCYPHOIDES Pat., Bull. Soc. Myc. Fr. **15**: 195. 1899. (Type.)
LENTINUS SUBSCYPHOIDES Murr., Mycologia **3**: 34. 1911. (Authentic material.)

Aside from the above indicated types and authentic material, the writer has studied large numbers of fresh specimens, and compared them with the types. These species are definitely identical. The following revised description is based on the data obtained.

*Pileus* "raw umber" with pallid margin, the margin which is involute

often colored "dull lavender" on the lower side, more rarely lavender colored also on the upper surface, or not infrequently the entire pileus similarly colored, the lavender tinge gradually disappearing, especially in old carpophores that have been dried out and revived by weather conditions several times, glabrous or faintly fibrillose-subtomentose, non-viscid, subhygrophanous, infundibuliform from the beginning, with an orbicular or irregular outline, often splitting radiately more or less deeply, or lobed, but more frequently entire if normally developed, 10–45 mm. broad.—*Lamellae* usually "dull lavender," becoming tan color, deep descendant-decurrent, somewhat arcuate in most specimens, the lavender color sometimes lacking from the beginning in the inner (rear) half of the hymenophore, usually eventually disappearing everywhere, very narrow (1 mm.), forking, close to usually crowded, rather thin, with acute edges when mature.—*Stipe* either flushed with lavender like the lamellae at the apex, or unicolorous, tan color all over, often with grayish fibrillosity, solid, eventually often hollow, often broadened into a discoid socle at the base, sometimes tapering from the base to the apex, simple, rarely once branching, central or eccentric, 17–40×1.2–4 mm.—*Context* dirty lavender violet all over, becoming tan color, or tan color from the beginning, or partly so, rather tough but very flexible, tougher in the stipe, reviving when wetted; thin; odor farinaceous, but rather weak; taste more or less bitter.

*Spores* (3.3)–3.5–6×2.5–3.5–(4)μ, short-ellipsoid to ellipsoid-oblong, non-amyloid, smooth, hyaline; *basidia* (1- 2-) 4-spored, 21–25×3.5–6.3μ; cystidia none or few, with the walls very slightly tough, noticeably thicker than in the basidia (about as thick as in the hyphae); cheilocystidia scattered, little differentiated, very versiform, inconspicuous; *gill-trama* regular, consisting of subparallel-subinterwoven, non-amyloid hyphae with a diameter of about 2–2.2μ, with very slightly thickened walls (0.5–0.7μ); they are somewhat irregularly interwoven and partly pigmented with a melleous, dissolved, intracellular pigment; *epicutis* formed by a trichodermium consisting of clavate or subclavate terminal hyphae, 15–32×3–9μ, mostly about 28×6–7μ (wall 0.5–0.7μ thick); *hyphae* of the stipe essentially longitudinally arranged but interwoven, hyaline, smooth, with 0.4–0.8μ thick walls, 2.5–5.5μ in diameter; all hyphae with clamp connections, hyaline to yellowish in iodine.

On logs of frondose trees such as *Nectandra coriacea*, *Theobroma cacao*, *Psidium guava*, *Cecropia peltata*, *Quercus virginiana*, etc. in tropical hammocks and plantations, gregarious, fruiting from September until December, possibly also earlier in the year, according to the rainy seasons, common everywhere within the area; Florida (tropical zone); Cuba, and through the Caribbean area to the Guianas and south to Brazil.

Material studied: FLORIDA: Dade Co., *R. Singer F 987*, *F 926*, *F 761*, etc. (FH); *R. Thaxter*, det. Singer (FH).—GUADELOUPE: type and authentic material of *L. scyphoides* (FH); Pointe

Noire, 2 collections in the Patouillard Herbarium (FH).—CUBA: Josephina, *Wright, 44,* type of *Marasmius purpurascens* (FH); *165* (FH).—PUERTO RICO: *J. R. Johnson, F 18715,* authentic material of *L. subscyphoides* Murr.[5] (FLAS).—TRINIDAD: Port of Spain, on old termite nests, *R. Thaxter,* det. R. Singer, (FH).—FRENCH GUIANA: *Leprieur 1041,* type of *Panus cantharelloides* (FH).—BRAZIL: Rio Grande do Sul, Serro Azul, *J. Rick, 402,* det. Singer (FH).

The oldest of the above species is *Panus cantharelloides* Mont. which was transferred by Patouillard to *Trogia*, by Murrill to *Panellus*. Though this may fit into the Earle-Murrill conception of *Panellus* which is artificial, it does not agree with the characters of *Panellus* Karst. as outlined by the writer. The spores are non-amyloid and the stipes are more vertical and elongated than in *Panellus*. I accept Patouillard's transfer as correct, since *P. cantharelloides* has all the important characters of a group of agarics one of which appears to be the type of the genus *Trogia*. Other species of *Trogia* are *T. buccinalis* (Mont.) Pat. from South America, with less crowded lamellae; *T. discopoda* (Pat.) Pat., and *T. violaceogrisea* (Henn.) Pat. from the Congo to Liberia and Cameroun; also *T. aplorutis* (Mont.) Fr. and *T. infundibuliformis* Berk. & Br., and others.

*Trogia cantharelloides* (Mont.) Pat. is the first species of *Trogia* discovered on the North American continent (see Singer, Mycologia **36**: 554. 1944). The type is strongly split and lobed, and rather large in size while the Brazilian specimens are also large but have an entire margin; the majority of the specimens from the Antilles and Florida are moderately large and entire. Neither these small differences nor the presence and extent of the lavender color have the slightest taxonomic importance.

*Trogia*, as a genus, differs from *Lentinus* (to which Patouillard referred most of the species in the beginning, transferring them gradually after 1900 and especially after 1914) in the absence of strongly thickened hyphal walls and in the non-cylindric shape of the spores, or at least a large number of spores in each preparation, in the constantly entire, forking lamellae, in the slender shape of the carpophores, and to a certain degree, in the structure of the cuticle. It differs from *Panus* in the absence of thick-walled cystidia, in thinner context, a different structure of the cuticle, and forked lamellae; it is distinguished from *Clitocybe* in the constantly rather tough, revivescent context and in the periodical formation of spores evidenced by the frequency of sterile hymenophores in the *Trogiae*. It differs from *Nothopanus* in the colored hymenophores which are much narrower, more forked, decurrent, and in the presence of a much more well-developed stipe in all specimens, also in the presence of a trichodermium on the pileus.

The lamellae of *Trogia*, above the point where they join in forking, are so

[5] I have not studied or compared with my fresh material the type of *L. subscyphoides* but a macroscopical check made in 1943 (NY) revealed specimens of the general external appearance of *Trogia cantharelloides*, exactly as described above.

close to each other in many instances that they appear to be broadened along the edge, and obtuse, or even canaliculate as described and illustrated by Montagne for *Cantherellus aplorutis* Mont. This condition has nothing to do with the reticulate venation of the hymenophores in the chiastobasidial Cantharellaceae (*Gomphus*, etc.) which are fundamentally different in their biology (humicolous and non-revivescent vs. lignicolous and revivescent), color of the spores (yellow to green vs. white), size of the spores and basidia (voluminous against small), diameter of the hyphal wall when compared with the diameter of the hyphae (large against small), consistency (soft-fleshy and thick against tough and thin), and the volume of the carpophores (large against small). There is not the slightest relation between any representative of the Cantharellaceae and the Trogias. They must be transferred to the Tricholomataceae, where they are closest to *Lentinus* and *Panus*, perhaps *Clitocybe*. They should not be confused with the meruliaceous genus *Plicatura*.

LENTINULA DETONSA (Fr. ?) Murr., Mycologia **3**: 28. 1911. (Authentic material.)
ARMILLARIA BORYANA Murr., Bull. Torr. Bot. Cl. **66**: 31. 1939, (*non* Berk., *Agaricus*). (Authentic material.)
ARMILLARIA RAPHANICA Murr., Mycologia **35**: 422. 1943. (Type.)
GYMNOPUS ALLIACEUS Murr., Mycologia **35**: 425. 1943. (Type.)

All the above named species are identical with each other, and at the same time, with *Lentinus cubensis* Berk. & Curt. *L. detonus* Fr. which would be the oldest of the names available, is very doubtful as far as the description is concerned, and if good type specimens do not exist, this name has to be abandoned.

*Lentinus glabratus* Mont., Pl. Cell. Cuba, p. 424, 1842 would also antedate *L. cubensis*, but the type at Paris "resembles *Lentinula detonsa* but differs in having decurrent gills and brown marginal hairs" (Murrill). Authentic material at Kew "seems referable rather to *Lentinula detonsa*" (Murrill). On the basis of this material, Berkeley determined a Cuban agaric, now found in Wright's Cuban Fungi (FH), as *Lentinus glabratus* Mont. The same species is also found in the Curtis Herbarium (FH). An analysis of these specimens shows that they are not *L. cubensis*, nor a *Lentinus* at all, but *Oudemansiella Canarii* (Jungh.) Höhn.

Consequently, I am using the name *Lentinus cubensis* B. & C. for the plant described below, on the basis of my own collections in Florida as well as of the types studied.

*Pileus* white, glabrous and smooth, or very minutely diffract to rimulose-subsquamulose on the disc, remaining glabrous and white on the margin, otherwise inclined to turn pale buff or pale tan in age, sometimes with 1–2 concentric zones, sometimes with fine ferruginous spots like those of

*Collybia maculata*, with a circular or ellipsoid outline, convex, then usually flat, eventually often depressed in the center, with initially incurved to subinvolute margin, occasionally with velar appendages, 50–80 mm. broad.—*Lamellae* white, whitish when fresh, often somewhat discolored in age or on drying, close to crowded, sinuate-adnexed to adnate, never distinctly decurrent, sometimes rounded-adnexed, and in age usually tending to separate from the apex of the stipe, arcuate-linear, narrow (2.5–3 mm. broad), entire to eventually often perpendicularly splitting with the edges, consequently appearing toothed; spore print white.—*Stipe* pale pinkish cinnamon, white at the apex, eventually concolorous, the base often darker brownish in age, subglabrous at apex, subsquamulose below, with 0–3 "velar" belts similar to those of *L. tigrinus*, curved, more rarely straight, central to eccentric, equal or enlarged at the apex, or tapering downwards, the apex often short-striate in continuation of the lamellae, 22–50×4–10 mm.—*Context* white, unchanging when broken, rather tough fleshy when quite fresh, especially in stipe, softer in pileus but becoming almost leathery in age; taste of garlic; odor none, or slightly alliaceous.

*Spores* (4.2)–5.5–6×2–2.8μ, smooth, hyaline, non-amyloid, cylindric; *basidia* 17–25×3.5–4.5μ, 4-spored; basidiols (cystidiols?) fusoid; *cystidia*, pseudocystidia etc. none, but sometimes some hypha-like bodies are found projecting between the basidia (16–24×3–4.5μ); *trama* of lamellae regular, homogeneous, consisting of non-amyloid, smooth, filamentous, hyaline, somewhat interwoven hyphae; their walls 0.6–1.8μ thick; their septa with clamps; *cuticle* dense, consisting of hyphae with very variable diameter, intricately interwoven.

On logs of *Quercus laurifolia*, *Q. Catesbaea*, *Sloanea Massonii*, *Freziera undulata*, *Morisonia americana*, *Daphnopsis caribaea* etc. Gregarious to subcespitose. Fruiting from April until October. From Florida to Louisiana, and West Indies.

Material studied: FLORIDA: Gainesville, *W. A. Murrill* (F 17944, etc.) (FLAS); *R. Singer* (*F 2188*, FH), also numerous other collections at FLAS from Alachua, Columbia, Marion Co., Fla.—LOUISIANA: *Langlois*, comm. Lloyd (FH).—CUBA: Numerous collections, among them the types of *L. cubensis* and *L. proximus* (FH).—MARTINIQUE: det. Patouillard, *477* (FH).—GUADELOUPE: det. Patouillard, *33P*, *55P*, *58P*, *666* (FH).

## Fam. AMANITACEAE

AMANITA MAGNIVELARIS Peck, Ann. Rep. N. Y. State Mus. **50**: 96. 1898. (Type, and numerous fresh collections.)

*Pileus* white, inclining to yellowish when dried, more rarely with a pale alutaceous disc, subviscid when wet, shining to subopaque when dry, with subacute to obtusely rounded margin which is split radially at times (in dry weather), convex, very often with a broad, low, very obtuse umbo, later almost flat, smooth and glabrous everywhere, without remnants of

the universal veil, 40–95 mm. broad, up to 27 mm. high.—*Lamellae* pure white, varying slightly orange-pallid, rather broad, sometimes partly serrulate at edges, quite free to sinuate-free with faint decurrent lines, medium broad to rather broad (3–7 mm.). with the lamellulae either suddenly emarginate (the shorter ones), or gradually attenuate (especially the longer ones), subclose to crowded; spore print pure white when fresh. —*Stipe* pure white, or in age with yellowish stains, subglabrous to entirely white fibrillose-flocculose, solid, sometimes finely banded in lower half, with a slight elongated or subglobose bulb or without it (25–35 mm. in diameter if present), equal or slightly tapering upwards, with distinct annulus and volva, 60–150×11–20 mm. (not counting the volva); annulus attached 6–11 mm. from the very apex of the stipe, fimbriate at the margin, tender-membranaceous, white, distant and pendulous (shirt-like), tending to stain yellowish in age, somewhat striate above; volva white to whitish, well developed, loosely saccate with broad free or applicate upper portion, firmly attached below, large (25–75×25–35 mm.), somewhat fragile above but not friable, rather thin in upper third.—*Context* pure white, unchanging on bruising; odor somewhat of old wine barrels or lye, or carpenter's glue, or Camembert cheese, or chloride of lime.

*Spores* medium-sized and neither oblong-cylindric, nor globose-subglobose, amyloid, smooth, 8–12×6.2–8.8μ ($\frac{8-8.2-9.3-9.5-10-10-11-11-12}{6.5-6.2-6.5-7.2-7-8-7.5-8.8-8}\mu$), *basidia* 32–41×12–14μ, 4-spored; *cheilocystidia* vesiculose, 17–22×10–19μ; *trama* of lamellae bilateral in youth, rather intermixed in age; *hyphae* without clamp connections.

KOH, immediately "amber yellow," "wax yellow," "strontian yellow" on context and all surfaces, especially on the stipe and annulus; positive even in carefully preserved not too old specimens in the herbarium.— Methylparamidophenol, negative, only interior of the base sordid drab.— Phenol and formaline, negative.

On poor, sandy or rocky soil under *Pinus* (*P. strobus*, *P. taeda*, etc.), *Quercus*, or *Betula* (various species), fruiting from April until October, in the northern part of the area mostly from June until September. Eastern United States from New England to North Florida, rather common.

This is often determined as *A. verna* (Bull. *ex* Fr.) Pers. *ex* Secr. and not admitted (listed as doubtful) by Murrill in North America Flora (1914), although admitted for Florida (1938); evidently the specimens referred there were correctly determined. In the writer's opinion, this is definitely different from anything he has seen in Europe, and not closely related to the *Phalloides*-group. This opinion can now easily be checked, since we have a very selective and simple chemical test for this species. I do not

know any other *Amanita* that reacts equally fast and strongly yellow with KOH.

VENENARIUS SUBMUTABILIS Murr., Mycologia **35**: 428. 1943. (Type, and authentic material.)

*Pileus* white, rarely slightly palest cream color in age, subviscid or viscid in wet weather, smooth except for a 2–10 mm. broad marginal zone which is sometimes indistinctly striate in age, often faintly warty-rugose on the disc, sometimes naked but usually with very thin, rather few, broad, membranous but not friable white to palest pinkish-grayish white patches from the universal veil, with subobtuse to broadly rounded margin, convex, eventually rather flat, (40)–60–100 mm. broad.—*Lamellae* white, with flocculose edges, rather broad to very broad (up to 14 mm.), ventricose, close to crowded, deeply sinuate with decurrent, linear sooth or completely free; spore print pure white when fresh.—*Stipe* white, solid, eventually partially hollow, about as long or longer than the diameter of the pileus, (40)–60–130×11–20 mm. (breadth measured just above the bulb which is up to 30 mm. in diameter), usually equal above the bulb, annulate, volvate; annulus white, pendulous, persistent, striatulate above, attached 5–20 mm. from the very apex of the stipe; volva thick and cup-shaped-saccate, deeply attached at the base, somewhat thinning in the free upper portion which therefore may eventually disappear leaving a bulb of the appearance of that of *Amanita citrina*, but not friable as in *A. chlorinosma*. —*Context* white, turning a beautiful intense pink ("thuilite pink" Ridgway, in *A. mutabilis* to "Eugenia red") when bruised; odor usually none (so in most of the hundreds of specimens I have tested in all ages as long as they are quite fresh, slight and pleasant of *Suillus variegatus* or "oily" according to Beardslee for *A. mutabilis*).

*Spores* 10.5–13.7×6.5–7.5μ, hyaline, amyloid; *basidia* 43–46×10.5–11μ.

KOH, formaline, and aniline: negative.—Methylparamidophenol, negative.—Phenol accelerates the change to pink.

Under *Pinus palustris*, and *P. taeda* on moist sandy ground, also under *Quercus*, on sandy ground, fruiting from July till October. From North Carolina to extratropical South Florida, probably also west to Alabama.

This species is common in Highlands Hammock State Park, Fla., and rather frequent in and around Gainesville. Neither the spores nor any other character I could discover separate this species from *A. mutabilis* Beardslee. *V. submutabilis* is a synonym of *A. mutabilis*.

Fam. CORTINARIACEAE

MARASMIUS SQUAMOSIDISCUS Murr., Bull. Tor. Bot. Cl. **67**: 151. 1940. (Type, and fresh material.)

LENTODIUM FLORIDANUM Murr., Mycologia **35**: 426. 1943. (Type.)
ARMILLARIA ALACHUANA Murr., Mim. Contr. Herb. U. of Fla. Agr. Exp. Sta., p. 12. 1938 *nom. nud.* (Type, and authentic materials.)

All these materials are identical with each other and, in addition, with an unpublished species of *Lepiota* (FLAS, coll. & det. W. A. Murrill). *Lepiota* may be the first genus that this species suggests when seen in the woods; there is, however no similarity with *Marasmius* or *Lentinus*, or *Armillaria*. As the following complete description shows, this has some characteristics of *Ripartites*. Consequently the combination **Ripartitella squamosidisca** (Murr.) Sing. is proposed. The other species become synonyms of it.[6]

*Pileus* white or whitish, the disc with suberect rusty to reddish brown, acute, later appressed squamulae which are then extremely like those of *Crepidotus calolepis*, non-viscid, the scales detersible, washed off by heavy rains, the margin glabrous and naked except for occasional traces of the veil, smooth, convex, eventually flat with the center often depressed, or shallowly umbilicate, with suborbicular outline, or sometimes lobed, diameter 20–50 mm.—*Lamella* white, eventually sordid white, entire, intermixed with lamellulae (polydymous), squarely adnate, to adnexed-subfree, never quite free, often with an adnate-decurrent tooth, or sinuate-emarginate, narrow (2.5–3 mm.), close to crowded, sublinear; spore print white.—*Stipe* on whitish ground whitish to whitish-brownish-squamulose to flocculose, the scales or floccons transversely elongated, minute to medium sized, the whole surface becoming eventually pale brown in the lower part of the stipe, naked and glabrous above the annular zone, straight or somewhat curved, central or frequently slightly eccentric, equal or slightly tapering upwards, or downwards, solid, then hollow, 15–40×2–5.5 mm.; base connected with thin, white, rhizomorphal strands. —*Context* white, unchanging, thin, inodorous, mild.

*Spores* 4–5×3.5–3.8μ, finely echinulate, broadly ellipsoid, non-amyloid,

[6] If it is possible, for an experienced observer, to "deposit," in a classification based on the Friesian macroscopical characters, a single species in four different genera in the herbarium, publish them in two different genera, and then have them all transferred to a genus belonging to a different family as soon as microscopical characters are used, it appears that that classification, aside from being the opposite of natural, is not practical at all, as it has been claimed to be. Similarly bewildering cases can be enumerated without limit (see our comments on *Oudemansiella Canarii*, and the list of synonyms, Mycologia **37**: 436. 1945; also *Rhodophyllus Farlowii* Sing., Farlowia **2**: 50. 1945; the synonymy of *Xerula chrysopepla*, see Mycologia **35**: 158. 1943, the unending confusion between *Collybia* and *Marasmius*, *Tricholoma* and *Clitocybe* (see Pap. Mich. Acad. **28**: 85–86. 1943), *Naucoria* and "*Galera*"). Why, then, do some taxonomists so stubbornly adhere to the Friesian scheme? If it is because we cannot offer anything perfect or foolproof in exchange, this reason may just as well be given forever. Determining agarics in the field with a handlens, and writing keys for this purpose, is definitely impossible. He who recognizes an agaric in a familiar fungus flora does so thanks to experience and the intuition that comes with it. The best way to gain this experience, is to study carefully both the external and anatomical characters of the agarics.

brownish-hyaline; *basidia* 19–33×4.5–7.5μ, 4-spored; *cystidia* of the *Melanoleuca*-type; *trama* of the gills regular, consisting of subinterwoven, hyaline, long-cylindric hyphae with small diameter and thin, non-amyloid walls; *hyphae of scales* filamentous to short-cylindric (to as broad as 12× 11μ), in subparallel chains forming strands; *hyphae of cuticle* repent, somewhat radially arranged, hyaline; all hyphae with clamp connections.

On trunks, logs, roots, detritus, also on buried wood, mostly on *Nyssa*, *Persea*, *Quercus*, and other frondose trees in low hammocks as well as in flatwoods, cespitose to gregarious, fruiting mostly from August till November. Thus far observed in Florida, in the extratropical zone rather frequent (Highlands Hammock State Park, and in Alachua Co.), and Brazil.

NAUCORIA ALACHUANA Murr., Lloydia **5**: 149. 1942. (Type and co-type.)
PSILOCYBE ALACHUANA Murr., Lloydia **5**: 155. 1942. (Type.)
GALERULA SEMIGLOBATA Murr., Mycologia **35**: 531. 1943. (Type.)

*Spores* 6.7–9×3.5–5.3μ, smooth, with moderately thick wall, brownish-melleous (not rusty), reniform- to subglobose-reniform; *basidia* 13.5–26× 6.7–7.2μ, 4-spored; cystidia cheilocystidioid, near the edge, rare; the *cheilocystidia* 32–65×6.8–16μ, mostly around 49×7.5–11.5μ, exceptionally as small as 28×5μ, hyaline, often slightly brownish at the base, smooth, numerous, making the gill edge heteromorphous, clavate or with vesiculose apex and thin base, more rarely versiform, subcyclindric with ventricose portions etc., apex always broadly rounded; gill trama regular, consisting of elongated, in accumulations brownish-hyaline hyphae; *cuticle* a thick layer of erect dermatocystidia forming a palisade; *dermatocystidia* most frequently subulate, also ventricose near the middle, more rarely vesiculose or broader above, with broadly rounded apex, brownish below, hyaline above, 22–87×8–20μ, mostly 46–70×9–10μ; with no or little pigment incrustation; all hyphae with clamp connections.

The above data prove that all the characters, color, shape and size of the spores, absence of a germ pore, size of the basidia, shape and character of the cystidia, the palisade of dermatocystidia on the surface of the pileus, the presence of clamp connections, and also the macroscopical characters are those of *Naucoria* (Fr.) Quél. em. Singer (1936), including such species as *N. centunculus*. This means that the name *Naucoria alachuana* Murr. should be accepted, and the two other names should be rejected as being later synonyms.

### Fam. STROPHARIACEAE

AGARICUS HAEMATITES Berk. & Curt., (Proc.) Am. Acad. **4**: 117. 1860. (Type.)
AGARICUS FLAVOLIVENS Berk. & Curt., Proc. Am. Acad. **4**: 117. 1860. (Type.)

AGARICUS MUSAECOLA Berk. & Curt. Journ.) Linn. Soc. **10:** 291. 1868. (Type.)
AGARICUS PROTEUS Kalchbr. *apud* Thümen, Flora *59:* 424. 1876. (Type.)
CREPIDOTUS PSYCHOTRIAE Pat., Bull. Soc. Myc. Fr. **18:** 173. 1902. (Type.)
CREPIDOTUS BAMBUSINUS Pat., Journ. de Bot. **5:** 309. 1891. (Type.)

All these species were described as belonging to *Crepidotus*, but are different. They have the following characters in common: pleurotoid habit; whitish to purplish—fuscescent color of the pileus; purplish brown to sepia colored spore print; small size; spores with distinct germ pore, lentiform (compressed frontally), with double wall which is smooth, their length around 6.5$\mu$; cheilocystidia distinct but rather small, ventricose below, ampullaceous or with a slightly capitulate apex, hyaline numerous; cystidia none; dermatocystidia none; epicutis of repent, thin, filamentous, hyaline hyphae; clamp connections present.

These characters would indicate a pleurotoid parallel, in the subtropics and tropics, of the more generally distributed genus *Deconica*, and this is exactly how Kühner has understood Patouillard's genus *Melanotus*. *Melanotus* Pat. has the same kind of relationship to *Deconica* as *Pyrrhoglossum* to *Gymnopilus*. On this basis, I think that *Melanotus* is a small, natural, autonomous genus, closely related to *Deconica*, and belonging to the family Strophariaceae Sing. & Smith. Consequently, the following new combinations are proposed.

**Melanotus haematites** (B. & C.) Sing. comb, nov.; **Melanotus flavolivens** (B. & C.) Sing. comb. nov.; **Melanotus musaecola** (B. & C.) Sing. comb. nov.; **Melanotus proteus** (Kalchbr. *apud* Thümen) Sing. comb. nov.; **Melanotus Psychotriae** (Pat.) Sing. comb. nov.; besides, there are two forms, well preserved and provided with ample notes, both of which belong to this genus, one from Tennessee, U.S.A., collected by D. H. Linder on corn (*Zea*); another one from Florida and Brazil, collected by R. Singer and J. Rick, on palms. I hesitate to describe these forms in spite of the fact that the substrata are new for this genus, considering the present uncertainty concerning the delimitation of the existing species and the value of the habitat in a group that has never been monographed. It is possible that the nature of the substratum, or at least its taxonomic position does not play a major role in the systematics of *Melanotus*.

AGARICUS CACAOPHYLLUS Berk. & Curt., Journ. Linn. Soc. **10:** 291. 1868. (Type).

This peculiar species has also been described as belonging in *Crepidotus*. It does however not belong in that genus, as the following notes will show.

Spores 6.8–7.2–(8)×4.8–5.2–(5.5)$\mu$, warty-rough, melleous, without plage (i.e. a smooth disc in the inner suprahilar zone, such as observed in

*Galerina*); basidia 21–24×5.3–7μ, 4-spored, entirely imbedded in a chestnut brown to melleous-fulvous, thick, tough, insoluble, resinaceous incrustation; cystidia (or perhaps merely basidioles, sterile because of the incrustation?), fusoid, the same size as the basidia, and likewise incrusted; cheilocystidia filamentous, very thin, often thicker beneath and ampullaceous above, 18–19×2–5.5μ (neck, if present, 2.2–2.5 μ in diameter), yellow in KOH; surfaces with KOH unchanging macroscopically; their anatomical structure impossible to determine with the material at hand; hyphae with clamp connections.

This is not a truly pleurotoid agaric, rather it exhibits a *Naucoria*-habit. The incrustation of the hymenial elements is unique, but it also makes observation of anatomical details rather difficult. Since only the type is known (its Curtis Herbarium part consisting of but one specimen and this is pressed flat and perhaps atypical). It does not seem advisable to erect a genus for this plant unless new collections in the West Indies add more data to the above description. The latter does not suggest any of the known genera in the brown spored agarics (Cortinariaceae, Strophariaceae).

# The Genus Phellorina

W. H. Long

(*Albuquerque, N. M.*)

This genus is closely related to *Dictyocephalos* Underwood and *Chlamydopus* Spegazzini, having numerous characters in common. It is widely but sparingly distributed over the world, varying in size of individual specimens and in size and characters of the experidia, but apparently all one polymorphic species. Usually only a few plants are found in widely scattered localities in any given area.

Phellorina Berkeley, London Jour. Bot., **2**: 521. 1843.

1845 *Xylopodium* Montagne, Ann. Sci. Nat. (3rd. ser.) **4**: 364.
1883 *Areolaria* Kalchbrenner, Ertek. Term. 11 no. **8**: 8.
1906 *Cypellomyces* Spegazzini, An. Mus. Nac. Buenos Aires **16** (ser. 3, 9): 25.

*Sporophore* epigeous, *Peridium* of 2 layers- an exoperidium and an endoperidium. *Exoperidium* verrucose, continuous with the stem cortex. *Endoperidium* coriaceous, continuous with the stem apex, becoming urceolate on maturity. *Stipe* dilated at apex into the endoperidium, long, stout, becoming woody. *Gleba* powdery, having capillitium, spores and persistent, fasciculate basidia. *Columella* none. *Spores* colored, globose, verrucose. *Basidia* bearing apically 1–4 spores on short sterigmata.
*Type locality*: South Africa.
*Distribution*: North America; South America; Africa; Asia; Europe; Australia.

Phellorina inquinans Berk. London Journal Bot. **2**: 521, 1843.

1845 *Xylopodium delestrei* Dur. & Mont. Ann. Sci. Nat. (3rd. ser.) **4**: 364.
1872 *Xylopodium australe* Berk. Jour. Linn. Soc. **13**: 171.
1875 *Scleroderma strobilina* Kalch. Grev. **4**: 74.
1880 *Phellorina strobilina* Kalch. Grev. **9**: 4.
1881 *Phellorina erythospora* Kalch. Bull. de l'Acad. Imper. des Sciences de St. Petersbourg **27**: 141–142.
1882 *Phellorina squamosa* Kalch. & MacOwan, Grev. **10**: 109.
1886 *Areolaria strobilina* Kalch. Ertek. Term. 11 no. **8**: 8.
1887 *Xylopodium ochroleucum* Cke & Mass. Grev. **15**: 95.
1890 *Phellorina californica* Peck, 43. Rept. New York State Mus.: 35–36.
1891 *Phellorina squamosa* Kalch. & MacOwan var. *mongolica* P. Henn. Engler Bot. Jahrbüch. **14**: 362.
1896 *Phellorina saharae* Pat. & Trab. Bull. Soc. Myc. de France **12**: 151.
1899 *Xylopodium bonacinai* Speg. An. Soc. Cient. Argent. **47**: 268–269.
1900 *Phellorina delestrei* (Dur. & Mont.) Ed. Fischer, E. & P. Nat. Pfl. **1**: 1xx, 334.
1902 *Lycoperdon erinaceum* Speg. An. Mus. Nac. Buenos Aires **8**: 56–57.
1903 *Phellorina leptoderma* Pat., Bull. Soc. Myc. de France **19**: 250.
1905 *Phellorina australis* (Berk.) Lloyd Myc. Writ. **1**: Lyc. Aust.: 11.
1906 *Cypellomyces argentinensis* Speg. An. Mus. Nac. Buenos Aires **16**: 25.
1909 *Phellorina argentinensis* (Speg.) R. E. Fries, Arkiv. för Bot. **8**: 25.
1912 *Phellorina erinacea* (Speg.) Speg. An. Mus. Nac. Buenos Aires **23**: 19.


FIGS. 1–4. *Phellorina inquinans*, ×1.

*Type species*: *Phellorina inquinans* Berkeley

*Sporophore* consisting of sporocarp, stipe and bulbous base. *Sporocarp* globose to pyriform, 1½–5 cm. tall by 2–5 cm. wide at top. *Exoperidium* white when fresh becoming cinnamon in age, scaly, scales imbricated or erect, top scales or warts often large, quadrangular to pyramidal, usually flat on tops, 5–12 mm. across by 4–12 mm. tall, scales smaller and more or less imbricated on lower half of sporocarp, dehiscing in irregular pieces. *Endoperidium* a cupulate or urceolate expansion of stem apex, coriaceous and permanent for ½ to ⅚ of length, remainder a thin fragile membrane which disappears on dehiscence of the exoperidium, shining, pinkish buff to light pinkish cinnamon to usually cinnamon. *Mouth* an indefinite, irregular apical opening 2–5 cm. wide, formed when the exoperidium dehisces. *Stipe* consisting of a definite 2-layered cortex, outer layer of flattened imbricated scales which are usually deciduous, inner layer of cortex not scaly, usually darker in color than the outer layer, pecan brown to walnut brown, deciduous; stem firm, woody solid, cinnamon after the shedding of cortex, terete or usually flattened, tapering to base, 2–5 cm. tall by 8–20 mm. thick at apex, by 1–4 mm. thick at base, often with fragments of cortex still persisting (fig. 9). *Bulb* firm, a hard mass of hyphae and sand, rarely with a volvoid top (figs. 7 & 9), 10–20 mm. tall by 15–20 mm. wide. *Volva* none. *Radicating base* often present, roots stout, 10–18 mm. long. *Gleba* cinnamon when mature. *Capillitium* scanty, flattened, sparsely septate, subhyaline. *Spores* globose, 5–7μ in diameter, average 6μ. *Epispore* tinted yellow, echinulate.

*Habitat;* solitary or in small groups, rarely twins from common base, in sand or clay soil, in open or in partial shade of desert vegetation.

*Distribution:* AFRICA: North Africa, in Lloyd Myc. Collections as *Phellorina inquinans:* Algeria, Moghar Fockhani Sud Oranais, ex Herb. Patouillard, *30998;* Tunisia, Bis-M'Cherga, *X. Gillot*, 1903, *30999*, March 1904, *31000*, 1906, *31001*. Tunis, region de Zaghouan, April 1903, *31002;* Ex Herb. Paris, scrap of gleba *58492;* Ex Herb. Patouillard in N. Y. Bot. Garden, slide and scrap, *58848 Union of South Africa* in Lloyd Myc. Collections; Stellenbosch, *A. Duthie, 30997;* Cape Prov. Malcomess, Knapdaar District, comm. *A. M. Bottomley*, April 13, 1924, *27629* as *Ph. inquinans*, *27632* as *Ph. strobilina:* Cape Good Hope, ex type at Kew, slide *58553* as *Ph. inquinans;* Branfort, *Dr. Schankan* comm. *A. V. Duthie* (*300*), April 1921, *30313* as *Ph. strobilina;* Grahamstown, *H. Becker*, *30702* as *Ph. strobilina. North Africa* in Lloyd Myc. Collections: Ex herb. Patouillard, slide *58473* as *Ph. leptoderma;* ex Herb Paris, scrap and slide, *58472* as *Ph. saharae;* Slides ex Berlin & Kew, *58554* as *Ph. squamosa.* Abyssinia, *P. Schweinfurth.* 1891, slides *58555* as *Ph. squamosa.*

ASIA: India, Said Circle, Hyderabad Forest Division, *S. N. Ratnagar*, Lloyd Myc. Col. *31007* as *Ph. inquinans:* Rohtak District, Rohtak, *S. Ahmad*, December 28, 1942, no *681* (Ahmad), no. 11176 Herb. Long, (1 plant) as *Phellorina* sp.; July 10, 1945, no. *1297* (Ahmad), *11094* Herb. Long (2 plants) as *Ph. strobilina.*

NORTH AMERICA: *Arizona*, Peach Springs, *N. C. Wilson*, in N. Y. Bot. Garden 1 plant as *Tylostoma* sp. *California*, Crutts, 22 miles north of Barstow, May 13, 1922, *I. M. Johnston*, *30314*, Lloyd Myc. Coll. as *Ph. inquinans. Nevada*, Reno, *P. B. Kennedy*, Lloyd Myc. Coll. *5632* as *Ph. inquinans. New Mexico*, Dona Ana County, Jornado Experimental Range about 28 miles east of Las Cruces on Highway 70, elevation 4150, *R. S. Campbell & L. Ellison*, no. *694*, August 27, 1829 1 plant as *Ph. strobilina; K. A. Valentine*, summer 1941, *10109* (2 plants); June-July, 1942, *10264*


FIGS. 5–7. *Phellorina inquinans*, ×1.

(4 plants); *W. H. Long*, November 12, 1938, *8348* (10 plants), October 2, 1939, *8404* (1 plant), October 3, 1939, *8421* (2 plants); *W. H. Long & David J. Stouffer*, September 7, 1941, *9586* (1 plant). Mesilla Park, in Herb. A&M College, comm. *H. L. Barnett*, May 16, 1939, *7765* (1 plant).


FIGS. 8–9. *Phellorina inquinans*, ×1.

Albuquerque, $5\frac{1}{2}$ miles north on Old Town Boulevard, elevation, 4950 feet, *W. H. Long*, June 18, 1941, *9359* (1 plant) in shade of *Populus wislizeni*. *Texas*. Travis County, Austin, on Colorado River near old dam site, elevation 650 feet, *T. Moberg*, May 15, 1935, *7698* (2 plants), *7701* (10 plant); near Austin in mesquite flats, *W. H. Long*, November, 1911, *4539* (8 plants). Burleson County, on Porter farm in Brazos River bottom, elevation 367 feet, *G. E. Altstatt* (no. *93*), May 29, 1935, comm. *Dr. Walter Ezekiel*, *4539* (8 plants), *8446* (2 plants). *Utah*. Grantsville, near Salt Lake City, *Dr. H. L. Shantz*, August, 1912, *11075* (2 plants).

MEXICO: Culiacan, *T. S. Brandegee*, 1904, Lloyd Myc. Coll. *31003* as *Phellorina* sp.

AUSTRALIA: Warrecknabel, *F. M. Reader*, December 1903, Lloyd Myc. Coll. *31004* and *31005* as *Xylopodium australe;* Murray Desert, New South Wales, slide ex type at Kew, Lloyd Myc. Coll. *58686* as *Xylopodium* australe; Sydney, New South Wales, *J. B. Cleland* (*25a*), Lloyd Myc. Coll. *30996* as *Xylopodium delestrei;* East Canfield, *J. T. Paul* (*203*), Lloyd Myc. Coll. *50104* as *Ph. inquinans*, scrap and slide ex type at Kew, Lloyd Myc. Coll. *58684* as *Xylopodium ochroleucum. South Australia, J. B. Cleland* (*787*), Lloyd Myc. Coll. *30316* as *Ph. strobilina.*

Figures 1–4 show plants with 4 different types of warts on the exoperidium, large type in figure 1, medium size in figure 2 and practically no warts in figure 3, all from the same collection, same date and same locality; while figure 4 shows a plant with large pyramidal warts. Figures 5–7 again show 3 types of warts, figure 6 has large pyramidal warts similar to figure 4 while figure 5 has smaller flattened warts, both 4 and 6 came from the same area as figures 1–4, figure 7 shows the flattened, small type of warts usually attributed to *Ph. inquinans*. These 7 figures show all stages of warts from the large pyramidal ones to very small ones yet all are undoubtedly the same species; plants with the large pyramidal warts have been called *Ph. strobilina* while those with the smaller less conspicuous warts are known as *Ph. inquinans*. Figures 7 and 9 show plants with the so-called volva, which is only a mass of sand and hyphae left in volvoid shape when the exoperidium separated from the basal bulb; such plants represent a condition on which Spegazzini (1906) based his genus *Cypellomyces*.

The various so-called species of *Phellorina* are based on the size of plants, size and characters of the warts on the exoperidium, but such criteria are worthless for differentiating species in this genus since such variations may be found in the same collection as is shown in figures 1–6; the glebal characters in all the proposed species are practically the same, there may be a few minor variations in size and color of the spore.

Many desert genera, such as *Dictyocephalos*, *Podaxon* and others have marked variations in size and shape of the plants and in the character and size of the warts, still but one and only one real species is found under each genus. *Dictyocephalos attenuatus* especially is a very variable species as to size, shape and markings of the exoperidium as is shown by Long & Plunkett (1940).

A careful study of the descriptions and figures of the species listed here as synonyms does not show any characters on which a valid species could be based, all are therefore reduced to synonymy.

*Phellorina macrospora* Lloyd (1913) does not belong to this genus, according to Long (1942) but is an immature, depauperate specimen of *Podaxon pistillaris*, while the plant figured by Lloyd (1917) in his Myc. Writings as *Phellorina strobilina* has been shown by Long & Plunkett (1940) to be a specimen of *Dictyocephalos attenuatus*.

ACKNOWLEDGMENTS

I am under many obligations to Mr. John A. Stevenson for loan of material and for very valuable aid on the bibliography and to Dr. Fred J. Seaver for loan of material.

## REFERENCES

AHMAD, SULTAN. 1939. The Higher Fungi of the Punjab Plains I, The Gasteromyceteae. Jour. Ind. Bot. Soc. **18**: 49.

———. 1941. Higher Fungi of the Punjab Plains III, The Gasteromycetes. Jour. Ind. Bot. Soc. **20**: 140–141.

BERKELEY, M. J. 1843. Enumeration of fungi collected by Herr Zeyher in Uitenhage. London Jour. Bot. **2**: 521–522.

CUNNINGHAM, G. H. 1932. The Gasteromycetes of Australasia XIV. The family Tulostomataceae. Proc. Linn. Soc. N. S. Wales **57**: 27–28, 33–35.

———. 1944. The Gasteromycetes of Australia and New Zealand. P. 193.

DE TONI, J. B. 1888. *In* Saccardo Syll. Fung. **7**: 143–146, 489.

FORQUIGNON, L. 1886. Les Champignons Superieurs. Chap. IV, Description de qualques genres exotiques appertenent aux Basidiomycetes. P. 155.

FRIES, R. E. 1909. Ueber einege Gasteromyceten aus Bolivia und Argentinien, Arkiv. för Botanik **8** (11): 25.

HENNINGS, P. 1891. Fungi Africani. Engler Bot. Jahrbüch. **14**: 362.

KALCHBRENNER, C. 1875. *In* Thuemen, F. von. Symbolae ad floram mycologicam australiae. Grev. **4**: 74.

———. 1883. Gasteromycetes novi vel minus cogniti. Ertek. Term. 11, no. **8**: 8.

———. AND COOKE, M. C. 1880. Australian Fungi. Grev. **9**: 4.

———. AND THUEMEN, F. 1881. Fungorum in itineri mongolica. Bull. Acad. Imp. Sci. St. Petersbourg **27**: 141–142.

MONTAGNE, J. C. 1845. Ann. Sci. Nat. (3 ser.) **4**: 364.

LLOYD, C. G. 1905. Myc. Writ. **1**: The Lycoperdaceae of Australia, New Zealand and Neighboring Islands: 10–11; 1904, Let. **1**: 3.

———. 1906. Myc. Writ. **2**: 308; 1909, **3**: 441; 1912, **4**: Let. **39**: 8.

———. 1913. Loc. cit. **4**: Let. **44**: 9; 1917, **5**: 734–736.

———. 1920. Loc. cit. **6**: 961, note 853; 1923, **7**: 1174, 1199–1200.

LONG, W. H. AND PLUNKETT, O. A. 1940. Studies in the Gasteromycetes I, The Genus Dictyocephalos. Mycologia **32**: 696–709.

LONG, W. H. 1942. Studies in the Gasteromycetes VI. Mycologia **34**: 532–535.

PETRI, L. 1909. Flora Italica Crypt. Pars **1**: Fungi, Gasterales. Fasc. **5**: 109–111.

SACCARDO, P. A. 1891. Syll. Fung. **9**: 279. 1895, **11**: 167; 1899, **14**: 267.

———. 1905. **17**: 238. 1912, **21**: 491–492.

SPEGAZZINI, CARLOS. 1902. An. Mus. Nac. Buenos Aires **8**: 56–57.

———. 1899. An. Soc. Cient. Argent. **47**: 268–269.

———. 1906. An. Mus. Nac. Buenos Aires **16**: 25.

———. 1912. Myc. Argent. Series VI, An. Mus. Nac. Buenos Aires **23**: 18–19.

# The Genus Poronia in India

SULTAN AHMAD

*(Government College, Rohtak, India)*

The genus *Poronia* belongs to the family Xylariaceae of the Sphaeriales. It is distinguished from other members of the family by the black carbonous perithecia embedded in a white fleshy hemi-spherical or discoid stroma borne on a long or short stipe. It is closely allied to the genus *Carnostroma* which, however, differs from it in having a club shaped form like *Xylaria*.

Of the fifteen definitely known species of the genus only five have so far been reported from India. Another species, *Poronia punctata* noted by Lloyd (1920) as reported from India has not been included by Butler and Bisby, probably through oversight. In addition to the already known species the writer has recently collected one new species and another (*Poronia leporina*) of rare occurrence from the Punjab which brings the total number of species in this country to eight.

In the following key two of the species, viz. *P. punctata* and *P. gigantea*, are omitted as the record of the occurrence of the former requires verification, while the latter is imperfectly known.

KEY TO THE SPECIES

Group 1. *Growing on dung*

Plants small, growing on rabbit dung ..... 1. *P. leporina*
Plants large, growing on horse dung ..... 2. *P. oedipus*

Group 2. *Growing in sand*

Single species ..... 3. *P. arenaria*

Group 3. *Growing on dead or burnt stems*

Plants small, hemispherical, of bright yellow colour ..... 5. *P. kurziana*
Plants large, discoid.
Whitish in colour ..... 6. *P. polyporoides*
"Ageratum violet" in colour ..... 7. *P. indica*

1. PORONIA LEPORINA Ellis & Everhart, Proc. Phill., p. 229, 1890.

Stipitate, avellaneous to wood brown in colour; stipe up to 3 mm long, 0.5 mm thick, concolourous or olive brown, expanding above into a discoid stroma up to 2.8 mm in diameter and mamillose from the very prominent perithecia with black projecting ostioles; context light brown; perithecia ovate-globose, 315×385$\mu$, 3–30 in a head; asci cylindrical, 8-spored, 10.5×100$\mu$, with paraphyses; spores black, uniseriate, elliptical, 7.5–9 ×8.5–16.6$\mu$, with a hyaline coat.

Jaggatpur, Gurdaspur Distt., August 12, 1938 (no. 335); Rohtak, Dec. 25, 1942 (no. 664), Jan. 14, 1944 (no. 846), Sep. 26, 1945 (no. 1476). On rabbit dung.

Distribution.—Europe; N. America; Ceylon; India.

This is a unique little species growing on rabbit dung. It is stated to be very rare. It is, however, very common in the Punjab plains but due to its very small size it easily escapes notice. *P. minuta* Petch is exactly the same plant and does not differ from the present species in any essential respect.

2. PORONIA OEDIPUS Montagne, Syll. Plant Crypt. p. 209.

Stipitate, large, stroma light brown but the stipe almost black; stipe simple or branched up to 4.5 cm. high and 0.5 cm. thick at the clavate swollen base, tapering upwards and expanding into a discoid stroma up to 0.5 cm. in diameter, at first concave and then plane or slightly convex, pierced by the black prominent ostioles, context white; perithecia ovate, sunk in the stroma; asci cylindrical, 8-spored, with paraphyses; spores uniseriate, elliptical, 26.5–29.5×15.5μ, almost black.

Jaggatpur, Gurdaspur Distt., Sept. 15, 1941 (no. 464). On horse dung. Pusa (E. J. Butler); Botanic Garden, Saharanpur (W. Gollan). On horse dung.

Distribution.—Cosmopolitan.

This species is easily distinguished from the closely allied species *Poronia punctata* in having a long clavate swollen stipe.

3. PORONIA PUNCTATA (L.) Fries.

As already pointed out Lloyd notes that this species has been reported from India. It is a fairly common species in Europe and America but its occurrence in India needs verification.

4. PORONIA ARENARIA Syd. et Butler, Ann. Myc. Berl. 9: 420, 1911.

Stipitate, stipe up to 6 cm. long, 2–7 mm. in diameter, clothed with "mars brown" mycelium enclosing large particles of sand, tapering downwards, enlarged above into a discoid stroma which is elliptic to spherical and 0.5–1.5 cm. in diameter, "mouse gray" in colour, context white; perithecia globose; asci cylindrical, 8-spored, 112×12μ with numerous paraphyses; spores uniseriate, elliptical, 7–8×14–16μ, black.

Chatrapur, Madras Presidency; August 29, 1904. On sandy dunes near *Casuarina equisetifolia*, leg. E. J. Butler, co-types in Herb. Crypt. Ind. Orientalis, New Delhi, 3 specimens in Herb. Ahmad (no. 503).

Distribution.—India. Known only from the type collection.

According to Sydow and Butler (loc. cit.) this species is closely related to *Poronia Doumetii* Pat. from Tunis, but differs in form, colour and spores. The writer has examined the co-types of *Poronia arenaria* and finds that they closely agree in form with *P. Doumetii* as shown in the photograph of the type made by C. G. Lloyd. The spores measuring 7–8 ×14–16μ also perfectly agree with those of the latter which measure

9×15μ. Although the close resemblance in the habitat, form and spores strongly suggests that the two plants are one and the same species yet it has been thought advisable to keep them separate until some authentic material of *P. Doumetii* is available for comparison.

5. PORONIA KURZIANA (Curr.) Lloyd, Myc. Writ. **6**: 939, 1920.

*Xylaria Kurziana* Curr. Trans. Linn. Soc. II. **1**: 129, 1876.
*Kretschmaria Kurziana* (Curr.) Sacc. Syll. Fung. **2** (Addenda ad vol. 1): 26, 1883.
*Kretschmaria truncata* Pat. Bull. Soc. Myc. Fr. p. 109, 1888.
*Poronia fornicata* A. Moeller.

Sessile or sub-sessile, of bright yellow colour when fresh but turning to "light ochraceous buff" in drying, solitary or caespitose, sometimes contiguous, 3.2–7.4 mm. in diameter, forming a convex hemispherical stroma which appears mamillose under a hand lens from the slightly prominent perithecia; context white; perithecia globose, 400–450μ; asci cylindric 8.5–10×110–120.5μ with numerous filiform paraphyses; spores uniseriate, elliptical 6–7.5×12.5–16.5μ, black.

Jaggatpur, Gurdaspur, August 15, 1941 (no. 415); and September 20, 1941 (no. 441); Ladhar, Sheikhupura, August 25, 1942 (no. 679); Sargodha, September 12, 1943 (no. 842). On dead and burnt culms of *Saccharum munja* Roxb. Leg. S. Ahmad.

Botanic Garden, Calcutta; on brick laid paths where fire had been burnt. Rainy season. Leg. S. Kurz.

Distribution.—Brazil; Venezuela; Uganda; India.

The original description of the fungus suggests that it was probably found growing on the ground, but in view of the literature on the point it does not seem to be correct. It appears that the brick laid paths were covered with some grass which was burnt by fire and that the plants were actually growing from the burnt roots and rhizomes of grass, the usual habitat. It is a very common species frequenting the same habitat as the next, but easily distinguished from all the other species of the genus in having a golden yellow hemispherical head. The plants which are generally caespitose are sometimes actually contiguous in the manner of a *Kretschmaria*. It is cited as *Kretschmaria Kurziana* (Curr.) Sacc. by Butler and Bisby (1931).

6. PORONIA POLYPOROIDES P. Henn., Hedwigia **40**: 340, 1901.

Stipitate, white when fresh, "tilleul buff" on drying; stipe 1–1.25 cm. long, 1.5 mm. thick, expanding above into a flat or convex disc, 3.19–9.2 mm. in diameter with an irregular margin, pierced by numerous prominent black shining ostioles; context white; perithecia globose or subglobose, 340μ in diameter; asci cylindrical, 8-spored, 6.6×92.5μ, with numerous paraphyses; spores uniseriate, elliptical, 4–5×8.5–10.5μ, black.

Jaggatpur, Gurdaspur, August 15, 1939 (no. 371); September 20, 1941 (no. 420). On burnt culms of *Saccharum munja* Roxb. Leg. S. Ahmad.

Botanic Garden Saharanpur, August 25, and September 20, 1901. On dead stem and on the ground. Leg. W. Gollan.

Distribution.—India.

This is the first time this fungus has been found since the type was found in India. It is a beautiful plant with white discoid, punctate stroma borne on a short or long stalk. This species I think is very close to, if not the same as, *Poronia ustorum* described by Patouillard from New Caledonia.

7. **Poronia indica**, sp. nov.

Stromatibus stipitatis; stipite ad 1 cm. longo, apice 2 mm. diam., basi attenuato, purpurascenti-caeruleo("purplish blue"), superne stroma violaceum ("ageratum violet") ellipticum vel sphaericum incrassato, 4 mm. diam., hyphis zona 60–80μ lata externa unicoloribus; disco ostiolis nigris dense papillato; contextu albo; peritheciis ovalibus vel globosis, 300–350μ diam., immaturis.

Stroma stipitate, stipe up to 1 cm. long, 2 mm. in diameter at the top, attenuated below, "purplish blue" in colour, enlarged above into an elliptical or spherical stroma, 4 mm. in diameter, "ageratum violet" in colour, the colouring matter uniformly distributed in the hyphae forming a distinct zone 60–80μ thick on the exterior; the disc bears on the surface numerous black papillate ostioles; context white; perithecia oval or globose, 300–350μ in diameter, immature.

Ladhar, Sheikhupura, August 6, 1944 (no. 1477); on a fallen piece of dead wood buried in sand; September 20, 1945 (no. 1490), on dead roots of grass (*Eleusine flagellifera* Nees); Gakkhar, Gujranwala, July 20, 1945 (no. 1480), on dead roots of grass (*Cenchrus biflorus* Roxb.).

This species is very close to *Poronia arenaria* Syd. et Butl. but differs in its smaller size, distinctive colour, and the papillate ostioles from this and all other known species. The habitat of this plant as growing on dead pieces of wood buried in sand and the dead roots of grasses suggests that probably *Poronia arenaria* and *Poronia Doumetii* grow in a similar way but with age the substratum gradually decays and is ultimately lost.

### IMPERFECTLY KNOWN SPECIES

The following species of Poronia described from India is based on immature material which is not available for study anywhere in this country. In the Herb. Crypt. Ind. Orientalis, New Delhi, there is a note in the box containing the specimens of this species "sent to Sydow for determination but never returned."

It has been thought best to include the original description of this

species in order that our present knowledge of the species of this genus in India may be readily accessible in a single paper.

8. PORONIA GIGANTEA Sacc., Ann. Mycol. Berl. **12**: 302, 1914.

"Stromatibus longissime stipitatis; stipite 18–20 cm. long. (cum sclerotio), 2.5–3 mm. diam., cylindrico leviter flexuoso. sursum sensim tenuato, glabro, sicco crebro longit. sulcato, nigricante, basi sclerotiacea nigricante nunc tuberiformi, 12–15 mm. diam. nunc elongata inaequali 4 cm. longa, 7–8 mm. cr. intus aeque ac stipite alba, coriacea; cupula discoideo-convexa circa 1 cm. lata alba, ostiolis papillatis, crebris nigris punctato-asperula infra concaviuscula, nigra, rugulosa; peritheciis ovoideis, 300–400$\mu$ altis; omnino immaturis, parietibus prima aetate fulvescentibus, matero coriaceo-molli immersis."

"Hab. in fimo putrescente Elephantis in silvis pr. Mundomuzhi in India merid. Augusto 1913 (M. S. Ramaswami no. 331). Quamquam exemplaria sint adhuc immatura. Species eximia videtur et tam a multo minori *Poronia oedipode*, quam ab aeque procera sed tomentosa, arenicola et sclerotio destituta *Poronia Ehrenbergii* P. Henn. distincta."

## BIBLIOGRAPHY

BUTLER, E. J., AND BISBY, G. R. 1931.—Fungi of India. Imp. Counc. Agr. Res. Monog. I. viii +237 pp. Calcutta.

LLOYD, C. G. 1920.—The genus *Poronia*. Myc. Notes No. 62: 937–940.

# New Peronosporaceae from China*

Lee Ling and M.C. Tai

During the period from 1942 to 1944, downy mildews occurred abundantly in the vicinity of Chengtu, West China, and aroused the interest of the writers in this group of fungi. Altogether 36 species belonging to the Peronosporaceae have been collected during that period. Of these, four proved to be unknown and are here described as new.

## Plasmopara Plectranthi sp. nov.

Maculis brunneo-flavis, angularibus, ad 5 mm. diam.; caespitulis niveo-floccosis, hypophyllis; conidiophoris 160–325$\mu$ altis, 5.7–9.9$\mu$ crassis, ramis 1–4-furcatis, rectangulis, furcis terminalibus 5.7–11.4$\mu$ longis, rectis, apice acutiusculis; conidiis ovatis vel oblongatis, rare late ellipsoideis, hyalinis, (17)–24.55–(33)$\mu$ longis, (14)–18.80–(24)$\mu$ latis.

Spots brownish yellow, angular, up to 5 mm. diam., bounded by the leaf veins; sporangiophores hypophyllous, forming a layer of white growth on the infected area, 160–325×5.7–9.9$\mu$, 1–4 times monopodially branched at right angles, ultimate branchlets straight, 5.7–11.4$\mu$ long, slightly acute at the tips; sporangia ovate to oblong, rarely broadly elliptical, hyaline, 17–33×14–24$\mu$, averages 24.55×18.80$\mu$.

On *Plectranthus amethystoides* Bentham, Chengtu, Nov. 9, 1943.

## Peronospora Thyrocarpii sp. nov.

Maculis pallide viridi-flavis, irregularibus; caespitulis hypophyllis, griseo-brunneis, inconspicuis; conidiophoris 370–840$\mu$ altis, 5.7–7.6$\mu$ crassis, hyalinis vel fuscatis, 5–7-ies dichotome ramosis; conidiis subglobosis vel late ellipsoideis, fuscatis (11)–16.03–(21)$\mu$ longis, (10)–13.30–(17)$\mu$ latis.

Spots light greenish yellow, irregular, mostly on the lower leaves of the host; sporangiophores hypophyllous, forming a grayish brown growth, inconspicuous due to the heavy growth of hairs on the host leaves, 370–840×5.7–7.6$\mu$, 5–7 times dichotomously branched, hyaline to light brown, ultimate branchlets straight or slightly curved; sporangia broadly elliptical to subglobose, light brown, 11–21×10–17$\mu$, averages 16.03×13.30$\mu$.

On *Thyrocarpus Sampsonii* Hance, Chengtu, March 15, 1943.

## Peronospora Artemisiae-annuae sp. nov.

Maculis viridi-flavis, irregularibus, plerumque in foliorum marginibus dispositis; caespitulis sparsis, hypophyllis, griseolis; conidiophoris 345–880$\mu$ altis, 10–14$\mu$ crassis, 4–7-ies dichotome ramosis; ramulis ultimis rectis, rectangulis, terminalibus inflatis; conidiis ovoideis vel ellipsoideis, griseo-brunneis, (24)–37.03–(46)$\mu$ longis, (14)–20.19–(24)$\mu$ latis.

Spots yellowish green, irregular, mostly on the leaf margin; sporangio-

* Received for publication from the Division of Cultural Cooperation, Department of State.

phores hypophyllous, forming a thin sparse grayish growth, 345–880×10–14μ, 4–7 times dichotomously branched; ultimate branchlets straight, arising at right angles, terminating with a swollen tip; sporangia nar-


FIGS. 1–4. Conidiophores and conidia. 1. *Plasmopara Plectranthi*. 2. *Peronospora Thyrocarpii*. 3. *Peronospora Artemisiae-annuae*. 4. *Peronospora Lycii*.

rowly ovate to ellipsoidal, usually with a short pedicel, grayish brown, 24–46×14–24μ, averages 37.03×20.19μ.

On *Artemisia annua* L., Chengtu, April 21, 1943.

**Peronospora Lycii** sp. nov.

Maculis pallide viridi-flavis, immarginatis, plerumque in foliorum marginibus dispositis; caespitulis hypophyllis, niveis, inconspicuis; conidiophoris 240–400μ altis, 12.9–17.2μ crassis, 4–7-ies dichotome ramosis, furcis terminalibus 11.5–20μ longis, 2–2.8μ crassis, curvatis, rare rectis, divaricatis; conidiis subglobosis vel late ellipsoideis, rare globosis, fuscatis, (19)–25.6–(33)μ longis, (16)–22.34–(25.6)μ latis.

Spots light yellowish green, margin indistinct, usually along the leaf margin; sporangiophores hypophyllous, forming an inconspicuous loose white growth, 4–7 (mostly 4) times dichotomously branched, 240–400×12.9–17.2μ, ultimate branchlets curved, rarely straight, arising at acute angles, 11.5–20×2–2.8μ; sporangia light brown, subglobose to broadly elliptical, rarely globose, 19–33×16–27μ, averages 25.6×22.34μ.

On *Lycium chinense* Mill., Chengtu, Jan. 10, 1944.

# Effects of Selected Properties of Soils on Growth of Sudan Grass[1]

F. L. Wynd and G. R. Noggle

*(Michigan State College, East Lansing, Mich. and Blandy Experimental Farm, University of Virginia, Boyce, Va.*

## INTRODUCTION

A description of the chemical characteristics of a group of soils near Midland, Douglas County, Kansas, has been published by Wynd and Romig (1), and by Wynd and Noggle (2). Wynd and Noggle (3, 4, 5) have reported the effects of these characteristics on the growth of oats and rye harvested at the jointing stage. These earlier papers were detailed studies of the effects of the base exchange capacity, degree of base saturation, total replaceable bases, exchangeable calcium, magnesium, and potassium, organic matter, nitrogen, pH, calcium carbonate, and various fractions of phosphorus. The oats for these studies were grown on a group of fields during the winter and spring of 1940 and 1941. The rye was grown on a different group of soils in the same vicinity during the spring of 1941.

Comparisons of the effects of each of the several soil characteristics on the responses of both oats and rye suggested that growth was limited by the amount of total replaceable bases, while the content of nitrogen and carotene in the crop was governed by the amount of nitrogen in the soil.

The most satisfactory soils in this area for the production of oats and rye harvested at the jointing stage were characterized by relatively large amounts of replaceable bases, chemosorbed phosphorus, and nitrogen. The results of these earlier studies suggested that it might be possible to rate comparatively the values of the soils in this area for the production of immature grasses by the determination of a few major characteristics of the soil.

The purpose of the present paper is to report the relationships between a selected group of soil characteristics and the growth of Sudan grass.

## MATERIALS AND METHODS

Sudan was grown on a group of 10 soils in the vicinity of Midland, Douglas County, Kansas, during the summer of 1943. None of these soils was included in any of the previous studies. The crops were harvested at, or just before, the jointing stage. The determinations of the base exchange capacity, total replaceable bases, percentage base saturation, and nitrogen were accomplished by the methods described in the previous papers (1, 2, 3).

[1] The expenses incurred by the present study were borne in part by a grant from the Cerophyll Laboratories, Inc., Kansas City, Missouri.

TABLE 1. *Field data for Sudan grass and "first bottom" soils.*

| Field no. | Soil type | Previous crop | Date planted | Date harvested | Age in Days | Growth stage | Color and condition |
|---|---|---|---|---|---|---|---|
| 305 | Medium sandy loam, First bottom. | Alfalfa, winter killed. | Aug. 7 | Aug. 26 | 19 | Unjointed. 10–12″ height. | Dark green. Excellent condition. |
| 306 | Heavy black loam. First bottom. | Corn, winter killed. | July 21 | Aug. 9 | 19 | Unjointed. 12″ height. | Dark green. A little leaf spot. |
| 309 | Heavy clay loam, slightly sandy. ½–3″ sandy river fill. First bottom. | Rye, flooded. | July 30 | Aug. 16 | 17 | Unjointed. 12″ height. | Medium green. |
| 311 | ½ black loam, second bottom. ½ medium sandy loam, second bottom. | Oats, corn. Flooded. | Aug. 18 | Sept. 11 | 24 | 5–10% jointed. 14″ height. | Light green. Spotty in sandy areas. |

TABLE 2. *Field data for Sudan grass and "upland" soils.*

| Field no. | Soil type | Previous crop | Date planted | Date harvested | Age in Days | Growth stage | Color and condition |
|---|---|---|---|---|---|---|---|
| 300 | Medium loam. Second bottom. Not subject to flood. | Peas | June 24 | July 23 | 29 | 20% jointed. 12″ ave. height. | Light to medium green. |
| 301 | Sandy loam. Upland soil. | Brome, winter killed. | June 3 | June 27 | 24 | Unjointed. 12″ ave. height. | Dark green, perfect condition. |
| 302 | Heavy black loam. Second bottom. | Peas | June 29 | July 21 | 22 | 22% jointed. 14″ ave. height. | Dark green, perfect condition. |
| 303 | Heavy black loam. Second bottom. | Peas | June 21 | July 21 | 30 | 41% jointed. 20″ ave. height. | Medium green. Small amt. of leaf spot. |
| 304 | Sandy loam. Upland, with clay sections. | Oats | July 2 | July 24 | 22 | 1% jointed. 10″ ave. height. | Yellowish green. Spotty in color and rank. |
| 307 | Gumbo. Second bottom. | Soybeans. Winter killed. | July 8 | Aug. 4 | 27 | Unjointed. 14″ height. | Dark-medium green. A little leaf spot. |
| 308 | Fine sandy loam, with river silt. | Corn and melons. Winter killed. | Aug. 5 | Aug. 25 | 20 | Unjointed. 10″ height. | Very light green. |

The field data are presented in tables 1 and 2, and the chemical data in tables 3 and 4. The number of each point in the figures is the last digit of the corresponding field number presented in the tables.

If for the data for both the "first bottom" and "upland" soils are pooled, very irregular distributions of points are obtained. The data for these

TABLE 3. *Growth of Sudan grass, and properties of "first bottom" soils.*

| Field no. | Nitrogen % | Base exchange capacity m.e. per 100 grams | Replaceable bases m.e. per 100 grams | Base saturation % | Yield lbs. per acre |
|---|---|---|---|---|---|
| 305 | 0.131 | 25.0 | 29.3 | 117 | 623 |
| 306 | 0.142 | 25.8 | 31.9 | 124 | 714 |
| 309 | 0.126 | 23.0 | 28.3 | 123 | 537 |
| 311 | 0.122 | 22.8 | 20.1 | 8 | 377 |

TABLE 4. *Growth of Sudan grass, and properties of "upland" soils.*

| Field no. | Nitrogen % | Base Exchange capacity m.e. per 100 grams | Replaceable bases m.e. per 100 grams | Base saturation % | Yield lbs. per acre |
|---|---|---|---|---|---|
| 300 | 0.127 | 18.4 | 14.4 | 78 | 680 |
| 301 | 0.228 | 22.6 | 19.0 | 84 | 737 |
| 302 | 0.140 | 18.3 | 12.5 | 68 | 838 |
| 303 | 0.141 | 18.8 | 13.6 | 72 | 1009 |
| 304 | 0.127 | 14.4 | 10.5 | 73 | 493 |
| 307 | 0.165 | 22.9 | 17.9 | 78 | 958 |
| 308 | 0.083 | 13.2 | 13.8 | 105 | 466 |

groups of soils are, therefore, presented separately in the graphs. The soils of this area have not yet been classified into definite series, and the types included in the present study are grouped together loosely as "first bottom" and "upland" soils. First bottom soils are subject to periodic flooding by overflow from the Kansas River and Mud Creek, while the upland soils rarely, if ever, are inundated by river overflow. Topographically, field number 311 is an upland soil, yet its chemical characteristics relate it to the first bottom group. The data obtained from this field are very irregular, and their erratic locations in the figures should not prejudice the reader.

## EXPERIMENTAL RESULTS

*Replaceable bases:* The data in table 1 and figure 1 show that a close relationship exists between the growth of Sudan grass and the amount of replaceable bases in the first bottom soils.

The data for the relationship between the amounts of replaceable bases in the upland soils and the growth of Sudan grass are not as consistent as those obtained from the first bottom soils. However, figure 2 shows that a recognizable positive relationship does exist. An inspection of the data in

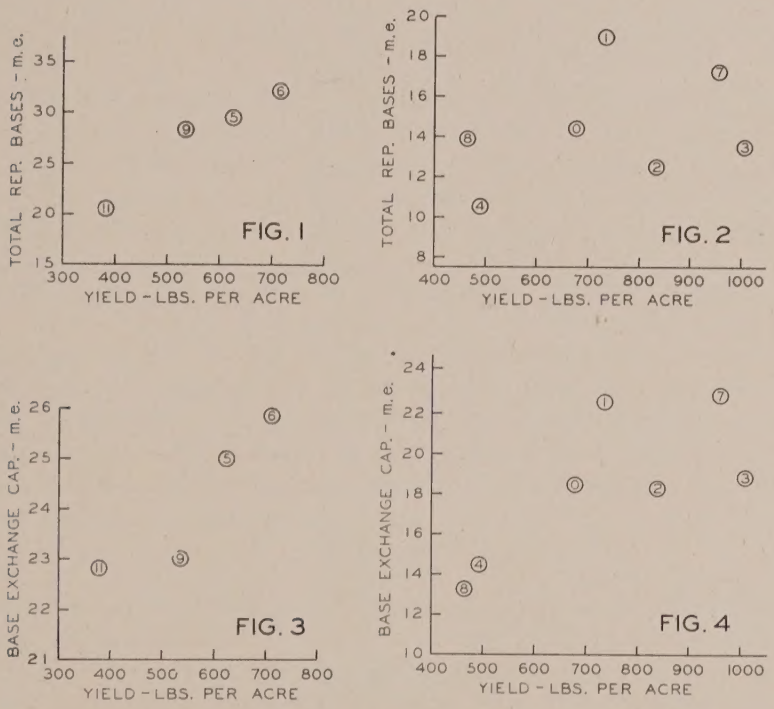



FIG. 1. Relationship between the growth of Sudan grass and the amount of replaceable bases in the first bottom soils.

FIG. 2. Relationship between the growth of Sudan grass and the amount of replaceable bases in the upland soils.

FIG. 3. Relationship between the growth of Sudan grass and the base exchange capacity of first bottom soils.

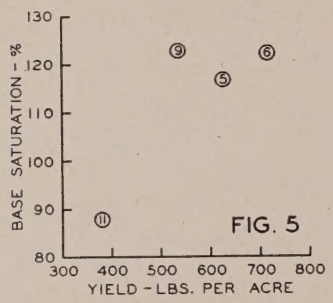
FIG. 4. Relationship between the growth of Sudan grass and the base exchange capacity of the upland soils.

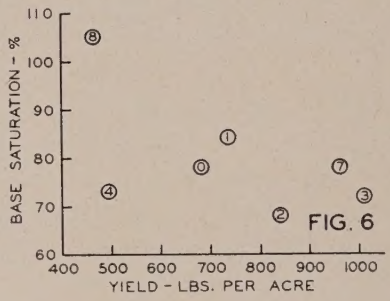
table 2 shows that the grass from fields 302 and 303 was well past the jointing stage at the time of harvest. The yields for these fields are, therefore, too large in comparison to other yields from this group of fields. These erroneous data are largely responsible for the irregular distribution of the points in figure 2.

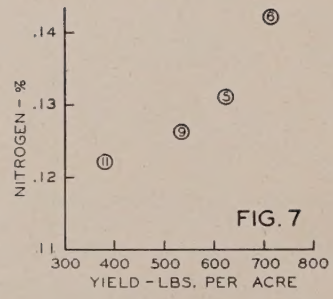
*Base exchange capacity:* Data in table 3 and figure 3 show a rather marked relationship between the base exchange capacity of the first bottom soils and the growth of Sudan grass. However, it should be noted that the

yield for field 309 falls in a somewhat erratic position with respect to the remaining points in the figure. Figure 1 showed that this yield fell regularly into line with the other yields when they are graphed with respect to the amounts of replaceable bases.

Data in table 4 and figure 4 show that the base exchange capacities of



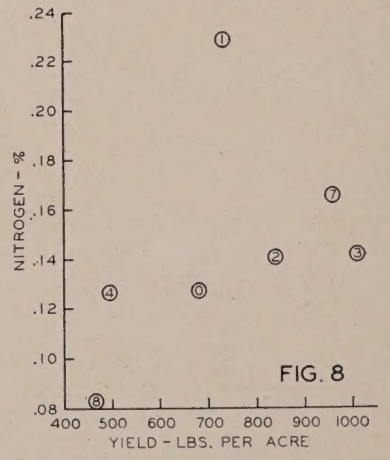




FIG. 5. Relationship between the growth of Sudan grass and the degree of base saturation of first bottom soils.

FIG. 6. Relationship between the growth of Sudan grass and the degree of base saturation of upland soils.

FIG. 7. Relationship between the growth of Sudan grass and the amount of nitrogen in first bottom soils.

FIG. 8. Relationship between the growth of Sudan grass and the amount of nitrogen in upland soils.

the upland soils are also positively related to the growth of Sudan grass. It should be recalled that the crops from fields 302 and 303 were harvested well after jointing was in progress, and therefore, the yields for these fields were too large in comparison with those from the remaining fields in this group.

*Degree of base saturation:* The data in tables 3 and 4 and figures 5 and 6 show that the degree of base saturation exerts no discernible effect on the growth of Sudan grass.

*Nitrogen:* The data in table 3 and figure 7 show a very definite correlation between the growth of Sudan grass on first bottom soils and the amount of nitrogen in the soil. The discussion below will show that this situation does not necessarily indicate an intrinsic relationship between growth and nitrogen.

The data in table 4 and figure 8 are particularly instructive. In general, there is a positive correlation between the growth of Sudan grass on the upland soils and the amount of nitrogen in the soil. Again, it should be recalled that the yields from fields 302 and 303 are too large. The yield from field 301, however, is very erratic with respect to the yields from the remaining fields of this group. Yet, figure 2 shows that yield is not erratic when the yields are plotted with respect to the amounts of replaceable bases. This fact suggests that the effect of the amount of replaceable bases is dominant over the effect of nitrogen in determining the growth of Sudan grass in the area studied. This statement is in agreement with the conclusions of Wynd and Noggle concerning the relative importance of replaceable bases and nitrogen on the growth of oats (3) and of rye (4). It is important to note that an entirely different group of soils was used for the study of each of these species.

## SUMMARY

1. A group of 10 soils in the vicinity of Midland, Douglas County, Kansas, was studied in respect to the association which existed between the total replaceable bases, base exchange capacity, degree of base saturation, and nitrogen and the growth of Sudan grass. These soils were loosely grouped as "first bottom" and "upland" soils.

2. A very positive correlation existed between the amount of replaceable bases and growth.

3. A positive correlation also existed between the amount of nitrogen present in the soil and growth, but this was true *only* if the amounts of nitrogen paralleled the amounts of replaceable bases.

4. The amount of replaceable bases is dominant over nitrogen in its effect on the growth of Sudan grass.

5. The degree of base saturation exerts no discernible influence on the growth of Sudan grass.

6. These results are in complete agreement with the authors' previous findings based on the study of oats and rye.

7. Different groups of soils in this area (i.e., "first bottom" and "upland") affect the growth of Sudan grass differently and the data may not be pooled, therefore, in the determination of correlations between soil characteristics and the growth of this species.

8. Although the results described are true for oats, rye, and Sudan grass grown in the vicinity of Midland, it is not known how generally applicable they would be for soils in other areas.

## LITERATURE CITED

1. WYND, F. L. AND ROMIG, J. R. Chemical characteristics of soils in the vicinity of Midland, Douglas County, Kansas, Soil Sci. **56**: 135–142. 1943.
2. WYND, F. L. AND NOGGLE, G. R. Associations between phosphorous fractions and other chemical components in soil. Soil Sci. **56**: 383–391. 1943.
3. WYND, F. L. AND NOGGLE, G. R. Relationships of chemical properties of soils near Midland, Douglas County, Kansas, to yield of oats harvested at jointing stage. Food Res. **10**: 408–414. 1945.
4. WYND, F. L. AND NOGGLE, G. R. Relationships of chemical properties of soils near Midland, Douglas County, Kansas, to yield of rye harvested at jointing stage. Food Res. **11**: 121–126. 1946.
5. WYND, F. L. AND NOGGLE, G. R. Relationships between fractions of phosphorus in the soil and growth of cereals. Food Res. (in press).